

Anatomy and phylogeny of the Chinese Major Carps *Ctenopharyngodon Steind.*, 1866 and *Hypophthalmichthys* Blkr., 1860

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Synopsis

The Chinese major carps, *Ctenopharyngodon* and *Hypophthalmichthys*, long held to belong to the subfamily Leuciscinae are each shown to represent separate lineages of a diphyletic Cyprinidae. This result is based on the analysis of 22 character complexes and the identification of supposed apomorphies. *Ctenopharyngodon* forms part of a monophyletic assembly termed the *squaliobarbine group* and *Hypophthalmichthys* is identified as the most derived member of the *abramine group*. The squaliobarbines are considered to be the sister group of all other barbelled Cyprinidae. The incongruity of character sets results in the presentation of two hypotheses for abramine intrarelationships. *Hypophthalmichthys* possesses a unique form of epibranchial organ; derived epibranchial structures are also identified in *Xenocypris* and *Abramis*. In the light of the data presented, the classification of the subfamily Leuciscinae is evaluated and many identifications of 'intergeneric' hybrids are falsified. Some comment is made concerning the phylogeny of barbelled cyprinids.

Introduction

The subjects of this study are the Chinese major carps, *Ctenopharyngodon* (the grass carp or white-amure) and *Hypophthalmichthys* (the silver and big-head carps). The object is to put forward a hypothesis of relationships of these taxa based on synapomorphic characters.

The major Chinese carps are of considerable economic importance as sources of protein and, in the case of *Ctenopharyngodon*, a control agent in restricting pond and canal weed growth. That these carps are primary-consumers and breed well in captivity are additional assets in their culture. Although there is much information on their biology—breeding, physiology, biochemistry and culturing, there are very few papers describing their anatomy. Of these only two or three authors have made statements regarding possible phylogenetic relationships.

Ctenopharyngodon is a monotypic genus included by Chu (1935) in the subfamily Leuciscinae. Berg (1949) considered the genus to be closely related to *Scardinius* and placed it in his all-embracing Cyprinini. Gosline (1978) placed *Ctenopharyngodon*, *Mylopharyngodon* and *Squaliobarbus* together, and although he was undecided whether they belonged to the subfamily Cyprininae or Leuciscinae, favoured retention in the latter. Even though the characters Gosline used for uniting these genera are considered by the present author to be a mosaic of plesio- and apomorphies, his hypothesis of relationships is not refuted in this study.

Hypophthalmichthys includes three nominal species, *H. molitrix* (Val.), *H. nobilis* (Richardson) and *H. harmandi* Sauvage. Oshima (1919) established the genus *Aristichthys* to contain *nobilis*, believing that differences in gill-raker form, abdominal keel length and pharyngeal dentition from those in *molitrix* were large enough to signify generic rank. Authors have been at variance in treating *Aristichthys* as a valid genus and many still regard *nobilis* as a species of *Hypophthalmichthys*. I would agree with the latter view. The taxa *molitrix* and *nobilis* possess unique synapomorphies and thus belong to the same higher category, ie. the genus *Hypophthalmichthys*. The species *H. harmandi* appears to have been overlooked by subsequent authors. To my knowledge it is known only from the type specimen from Hanoi, now in the Paris Museum.

Günther (1868) first introduced the category Hypophthalmichthina to contain *Hypophthalmichthys* which taxon Gill (1893) later recognized as a subfamily, the Hypophthalmichthinae. Regan (1911; 1922) thought *Hypophthalmichthys* to be related to *Barilius*—a suggestion refuted by Howes (1980). Kryzanovskij (1947) referred *Hypophthalmichthys* to the Leuciscinae on evidence derived from ontogenetic development. Ryabov (1973) agreed with this subfamilial placement, using as his evidence the viability of larvae produced by cross-breeding *Hypophthalmichthys* and *Abramis*—*Abramis* being considered a typical leuciscine. Gosline (1978), relying on a tri-lobed swimbladder as an indicator of this relationship, considered that there were 'clear indications of a cultrine derivation for *Hypophthalmichthys* and *Aristichthys*'. A tri-lobed swimbladder, however, has such a mosaic distribution throughout the Cyprinidae that it has no value as a character indicating shared common ancestry. Besides which, the third 'lobe' in *Hypophthalmichthys* is a mere constriction or 'tail' of the swimbladder and is variously developed in individual fish.

There has been only one study of the comparative osteology of the major Chinese Carps, that by Watanabe (1951). Although this author pointed out significant differences between *Ctenopharyngodon*, *Hypophthalmichthys* and *Mylopharyngodon*, and noted the possible taxonomic value of certain characters, he made no attempt to utilize them in formulating relationships.

Finally, it can be noted that artificial hybridization between *Ctenopharyngodon* and *Hypophthalmichthys* has been achieved and the morphology of the hybrids described by Berry & Low (1970).

The consensus of ichthyological opinion it would seem, is that the two major carps, *Ctenopharyngodon* and *Hypophthalmichthys* belong to the same subfamily, the Leuciscinae. My thesis is that they do not, but that each represents a distinct monophyletic lineage representative of a basic dichotomous division within the Cyprinidae.

Abbreviations used in the figures

AA	Anguloarticular	Aap	Adductor arcus palantini muscle
AEW	Anterior wall of epibranchial organ	Ah	Adductor hyomandibularis muscle

AMP	Anterior medial maxillary process	LEN	Supraethmoid notch for palatine head
BO	Basioccipital	LOF	Lateral occipital foramen
BOCB	Basioccipital cartilaginous bloc	ME	Mesethmoid
BOK	Basioccipital keel	MET	Metapterygoid
BON	Basioccipital notch	MF	Maxillary foramen
BP	Basioccipital pharyngeal process	MMP	Midlateral maxillary process
BUC	Buccal cavity	MP	Masticatory plate
CB	Ceratobranchial (numbered)	N	Nasal
CF	Ceratobranchial filaments	NC	Neural complex
CFE	Carotid fenestra	NS	Neural spine
CP	Coronoid process	OC	Intramural opercular canal
CPE	Cartilaginous preethmoid	OFT	Olfactory foramen
Dahm	Dorsal section of <i>adductor hyomandibularis</i>	OP	Operculum
DPTC	Dermopterotic canal	OPE	Ossified preethmoid
EB	Epibranchial (numbered)	PALH	Palatine head
EBD	Epibranchial duct (numbered)	PAR	Parietal
EBO	Epibranchial organ	PE	Preethmoid
EC	Ethmoid cartilage	PEW	Posterior wall of epibranchial organ
ECT	Epibranchial connective tissue	PF	Palatal fold
EOD	Epibranchial oesophagal duct	PFO	Prootic foramen
EOW	Epioccipital wing	PH	Pharyngeal bone
EP	Epioccipital	PHF	Fossa in pharyngeal bone
EPOP	Epioccipital process	Php	Pharyngeal pad
ER	Epibranchial rakers	PO	Preoperculum
ES	Extrascapular	POC	Preopercular canal
EXO	Exoccipital	PPSF	Prootic/parasphenoid fenestra
EXOF	Exoccipital flange	PRO	Prootic
F	Frontal	PS	Parasphenoid
FC	Frontal canal	PSAP	Parasphenoid ascending process
FF	Frontal foramen	PSCB	Parasphenoid keel
FIC	Internal carotid foramen	PTE	Pterotic
FJ	Jugular foramen	PTES	Pterotic spine
FII	Optic foramen	PTS	Pterosphenoid
FV	Foramen for trigeminal trunk	PTT	Posttemporal
FVII	Foramen for facial nerve trunk	PVP	Pterosphenoid ventral process
FVIII	Foramen for acoustic nerve	Q	Quadrate
FIX	Foramen for glossopharyngeal	SE	Supraethmoid
GR	Gill raker (globular)	SEW	Supraethmoid wing
HMF	Hyomandibular fossa	SM	Ceratobranchial sifting membrane
HYO	Hyomandibular	SO	Supraoccipital
HVII	Hyomandibular branch of VII nerve	SOCC	Supraoccipital crest
IC	Intercalar	SOP	Subopercle
ICF	Intercalar fossa	SOR	Supraorbital
IF	Infrapharyngobranchials (numbered)	SP	Sphenotic
IO	Infraorbitals (numbered)	V	Vomer
IOP	Interoperculum	Vahm	Ventral section of <i>adductor hyomandibularis</i> muscle
LE	Lateral ethmoid	VPSR	Ventral parasphenoid ridge
LEF	Lateral ethmoid/frontal fenestra		

Study material

All specimens used in the preparation of this paper are in the osteological and alcohol collections of the British Museum (Natural History). Lists of comparative material will be

found in previous publications (Howes, 1978; 1979). The catalogue numbers for specimens used in illustrating this work are given in the figure captions.

Comparison of selected characters in *Ctenopharyngodon* and *Hypophthalmichthys*

The following 22 characters were selected after a preliminary study had eliminated others which appeared to contain minimal information concerning their plesio- or apomorphic state (ie. intra- and interspecifically variable or mosaically distributed), and those which were considered to be symplesiomorphies. Guidance to the identification of plesiomorphic character state came both from previous studies on cyprinid phylogeny (Howes, 1978; 1979; 1980) and wider outgroup comparisons—outgroup in this case being other otophysans. Likewise, these earlier studies had led to the final selection of those characters which had previously been useful as phylogenetic indicators. Reasons for polarity assignment are present in the analysis below.

Selected characters: 1. Ethmo-vomerine region; 2. Pterospheonoid; 3. Parasphenoid; 4. Prootic; 5. Subtemporal fossa and associated musculature; 6. Dilator fossa; 7. Frontal; 8. Parietal; 9. Circumorbitals; 10. Supraoccipital; 11. Exoccipital; 12. Epioccipital; 13. Interocular; 14. Basisoccipital; 15. Posttemporal; 16. Opercular series; 17. Suspensorium; 18. Jaws; 19. Vertebral column; 20. Gill-arches; 21. *Adductor hyomandibulae* muscle; 22. Pectoral girdle.

Analysis of apomorph characters

1. *Ethmo-vomerine region*

Ctenopharyngodon (Fig. 1); supraethmoid broad and short with a shallow medial anterior notch and two lateral notches; preethmoids paired, largely cartilaginous; kinethmoid dorsally expanded; vomer widely V-shaped anteriorly; lateral ethmoid wall truncate.

Hypophthalmichthys (Fig. 1); supraethmoid broad and short with a deep medial notch; preethmoid single, small, completely ossified; kinethmoid rod-shaped; vomer thickened anteriorly and forming the floor of the median ethmoid notch; lateral ethmoid contains entire olfactory foramen in a bony tube; the lateral lamella is prolonged distally and curves ventrally; fenestra between the dorsal surface of the lateral wall and the frontal.

Both *Ctenopharyngodon* and *Hypophthalmichthys* possess a short, broad *supraethmoid* and depressed *mesethmoid*. This is hypothesized as the plesiomorph condition in cyprinids on the grounds of widespread occurrence. Within the Cyprinidae there are two basic forms of supraethmoid; (1) in which the anterior border of the bone is indented medially so as to accommodate the retracted kinethmoid (sometimes there may be indentations lateral to the medial one), and (2) where the supraethmoid is rostrally extended, its lateral border rounded and the tip of the extension bearing the median notch. These two types are illustrated in Fig. 2.

The first morphotype is that most commonly encountered in non-barbelled Cyprinidae (ie. Leuciscinae), whilst the second is that found in almost all barbelled Cyprinidae (ie. Cyprininae; *Barbus*, *Labeo* etc). In *Cyprinus*, *Carassius* and several members of the Gobioninae, although there is a prominent rostral process there is no, or but a slight, medial notch—the kinethmoid being attached to the base of the rostral process by a single ligament (oberes Rüsselband of Fiebig, 1931). This is similar to the condition in the Catostomidae where the supraethmoid is elongate and without a medial indentation.

A rostrally produced supraethmoid is the common condition amongst characoids and a comparison between the ethmoid region of *Brycon* and that of *Catostomus* shows a remarkable similarity. In siluroids the common condition, as in cyprinoids, appears to be one where the anterior ethmoid border bears a slight medial indentation. Within the cyprinids, although the extremes of the two ethmoid morphotypes can be readily appreciated, they are linked by a series of intergrades. Particular examples are in *Garra*

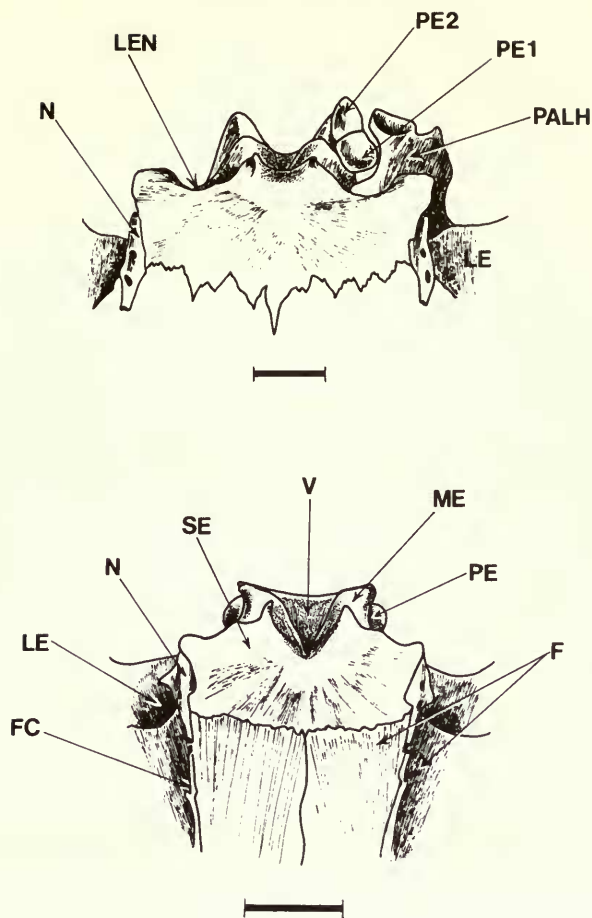


Fig. 1 Ethmo-vomerine regions in dorsal view: (upper) *Ctenopharyngodon idellus*; (lower) *Hypophthalmichthys molitrix*. Specimens BMNH 1888.5.15 : 25; 1895.5.31 : 22. Scales = 10 mm.

where the rostrally produced ethmoid shape is still discernible but the anterior border is deeply indented as in 'leuciscines'. Again, in some species of *Barbus* and *Schizothorax* the ethmoid is distinctly leuciscine-like. An extreme morphotype is encountered in *Semiplotus* and *Scaphiodonichthys* where the entire supraethmoid is almost vertically directed and it is the anterior border of the frontal which is medially indented. In general, it appears that cyprinids with a terminally placed mouth are those with a deeply notched ethmoid. On the other hand, the rostrally produced ethmoid is more characteristic of bottom feeding types where additional, almost ventral extension of the mouth is functionally desirable—as in *Semiplotus* mentioned above. Fink & Fink (1981) propose that a rostrally produced ethmoid is plesiomorphic for otophysans. It would appear that in cyprinids a supraethmoid with a slight, but broad rostral process is the plesiomorph state. This plan would offer the potential of producing either kind of morphotype. The variability of the supraethmoid in species of *Barbus* is discussed by Banister (in preparation). In that group, at least, the ethmoid appears to be a very labile structure and one responding to environmental influences.

In *Ctenopharyngodon* there are lateral indentations on either side of the medial supraethmoid notch (LEN, Fig. 1). These lateral notches accommodate the enlarged anterior condyles of the palatines. A similar feature occurs in *Squaliobarbus* and *Mylopharyngodon* and is considered synapomorphic.

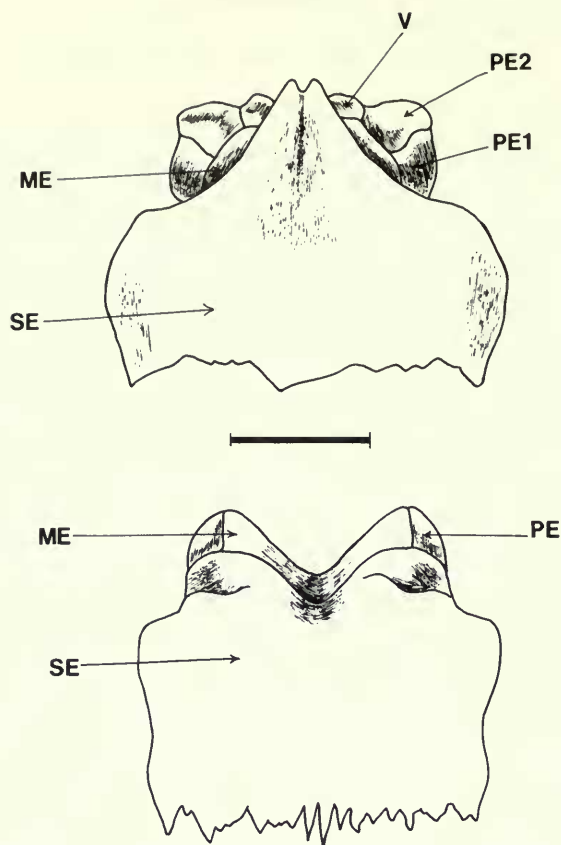


Fig. 2. Ethmo-vomerine regions in dorsal view: (upper) *Cyprinus carpio*; (lower) *Leuciscus cephalus*. Composite drawing of several specimens. Scale = 5 mm.

Concerning the posterior border of the supraethmoid, a transverse suture with the frontal appears to be the plesiomorph state. Only in some chelines is the posterior margin rounded or triangular and overlapped by the frontals (see Ramaswami, 1955*b*, fig. 3, and Howes, 1979). Amongst characoids the posterior ethmoid margin is triangular, that of siluroids is irregular, its medial part usually invaded by the anterior tip of the frontal fontanel.

A rod-shaped *kinethmoid* is considered the plesiomorph type (see Howes, 1978). I am unaware of any detailed study concerning the possible derivation or homology of the bone. Goodrich (1909) thought it to be a specialized part of the ethmoid. The common occurrence of a bifurcated kinethmoid suggests that there has been a phylogenetic ossification into a single unit of two premaxillary-ethmoid ligaments. There is no cyprinoid known to me in which these ligaments remain unossified in the adult, or even in larval stages, and which would represent the most plesiomorph state. In its various derived states the dorsal part of the kinethmoid may be expanded in a transverse plane, or the medial part of the bone may be swollen.

In *Ctenopharyngodon* the kinethmoid is dorsally expanded and thickened, a derived condition encountered in other cyprinid groups (eg. chelines; see Howes, 1979). In *Hypophthalmichthys* the bone remains as a slender rod.

Ramaswami (1955*a*) noted the absence of a *preethmoid* in *Hypophthalmichthys*, but this is not the case. A preethmoid cartilage is present, although minute and only fully ossified in the adult. Likewise, in other genera which Ramaswami (1955*a* & *b*) cites as lacking a preethmoid, I have found it as a poorly ossified element. Ossification of the preethmoid is variable; specimens of *Alburnus* show no sign of ossification until they are at least 56 mm SL;

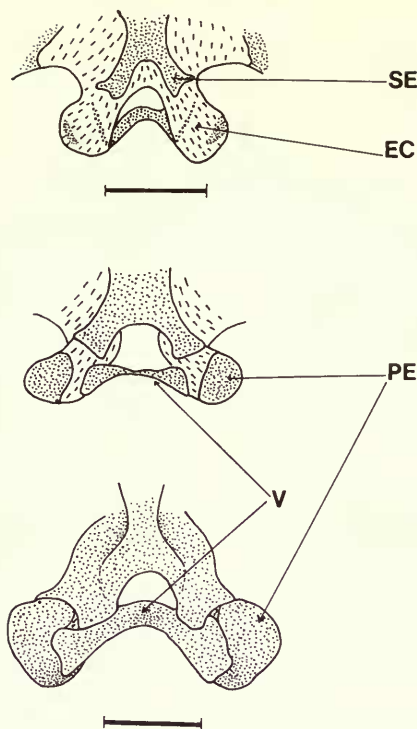


Fig. 3 Development of the ethmoid bloc in *Barbus* sp. Anterior view (top) from a specimen 13 mm SL; (centre) specimen 20 mm SL; (bottom) specimen 35 mm SL. Dashed areas = cartilage, stippled areas = ossification. Scales = 0.5 mm.

the preethmoid in *Oreoleuciscus* is entirely cartilaginous in a specimen of 114 mm SL. It is still recognizable as a preethmoid, being clearly differentiated from the ossified mesethmoidal process.

According to Alexander (1966) the preethmoid is an ossification of the antero-lateral process of the ethmoid cartilage (mesethmoid). He notes that in *Leuciscus* (= *Idus* of Alexander), the maxillary ascending process articulates with the preethmoid cartilage, and with the palatine *via* a cartilaginous insert (submaxillary meniscus of Alexander). Corroboration of Alexander's (1966) statement that the preethmoid is an ossification of the mesethmoid comes from an ontogenetic series of *Barbus* sp. (Fig. 3). In the smallest specimens, 12–14 mm SL, the preethmoid is not differentiated from the ethmoid cartilage and there is a sub-terminal ossification, in 20 mm specimens there is dorsal ossification of the lateral mesethmoid processes, greater area of terminal ossification and antero-lateral extension of the vomer. In specimens of between 25 mm and 27 mm SL there exists only a small area of cartilage between the mesethmoid, ossified preethmoid and vomer. At the 30–35 mm stage, the antero-lateral mesethmoid processes have contacted the now large and completely ossified preethmoids and the vomer. A lateral mesethmoid-vomerine fossa is formed and the preethmoid contacts the fossa *via* a thin meniscus of cartilage.

In all cyprinids I have examined, other than abramines (see below), the preethmoid is contained in a lateral fossa formed from the mesethmoid and the vomer (see Howes, 1978).

A lateral ethmo-vomerine fossa is lacking in *Abramis*, *Rutilus*, *Chondrostoma* and *Xenocypris*. In these taxa the vomer does not protrude laterally (see below) but extends forward; the preethmoid is extensive and covers the extended vomerine arm, contacting the mesethmoid only along its antero-ventral rim (see Figs 5A–D). The preethmoid is almost entirely cartilaginous with only the anterior tip being ossified in the case of *Abramis*, *Rutilus*

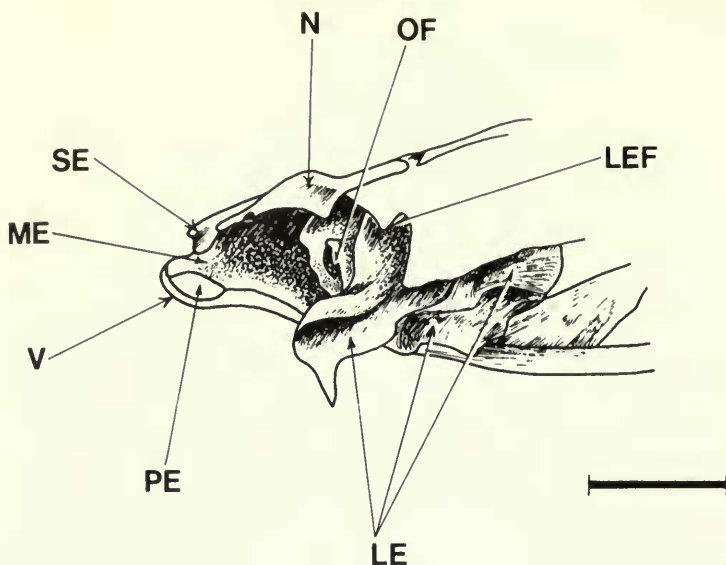


Fig. 4 *Hypophthalmichthys molitrix*, lateral view of ethmo-vomerine region. Specimen 1895.5.31 : 22. Scale = 10 mm.

and *Chondrostoma*, but a laterally ossified nub in *Xenocypris*. Although in *Hypophthalmichthys* there is a distinct reduction of the lateral fossa the preethmoid cartilage still contacts the lateral part of the mesethmoid (Fig. 4). Laterally, the preethmoid articulates directly with the palatine facet; only rarely is such a connection lacking (eg. *Ochetobius*); there is never direct contact with the maxilla. In some cyprinids, however, the preethmoid is extended anteriorly and may ossify into two parts. Such paired preethmoids were recorded in *Cyprinus* by Fiebiger (1931) as the lateral 'seitliches Knötchen' articulating with the palatine, and the anterior 'Sesamknöten' articulating with the maxilla. Paired preethmoids also occur in *Ctenopharyngodon* (Fig. 1), *Mylopharyngodon*, *Squaliobarbus* and some *Barbus* species. In these taxa, the anterior preethmoid is often unossified or only partially so. According to Ramaswami (1955a) it is the cartilage sandwiched between the maxilla and the preethmoid which ossifies to form a second preethmoid. However, in the taxa cited above, the additional, anterior ossification would appear to be within the original preethmoidal cartilage.

In gobiinids, cobitids and catostomids, the second preethmoid can be exceptionally well-developed and exists as an ossified strut (the septomaxilla of Regan, 1911 and Starks, 1926). Patterson (1975 : 501) reckons the preethmoids of cyprinoids to be neomorphs. As such they must be regarded as autapomorphic for Cyprinoidei. A single, lateral ossification of the ethmoid cartilage articulating with the palatine is hypothesized as representing the plesiomorph condition (see Howes, 1980).

The *mesethmoid* is usually a triangular bloc, its apex forming the rostrum of the entire ethmoid bloc. In those taxa with a medially indented supraethmoid, the mesethmoid becomes thickened anteriorly and forms a somewhat hour-glass shape. In some leuciscines, the mesethmoid is laterally excavated to such an extent that it is virtually a medial septum. The posterior wall of the mesethmoid cartilage is, in one group of leuciscines and some cyprinines, excavated to form the anterior myodome (see below).

The *lateral ethmoid* in cyprinids most often has a well-produced lateral wall with a broadly-triangular base; antero-medially it meets the mesethmoid and contains part of the olfactory nerve foramen in its leading edge; postero-medially it meets its fellow along the midline. In some cases the lateral ethmoids are indented into the mesethmoid cartilage so as to form an *anterior myodome*. Even though, as in aspinines, the anterior myodome extends

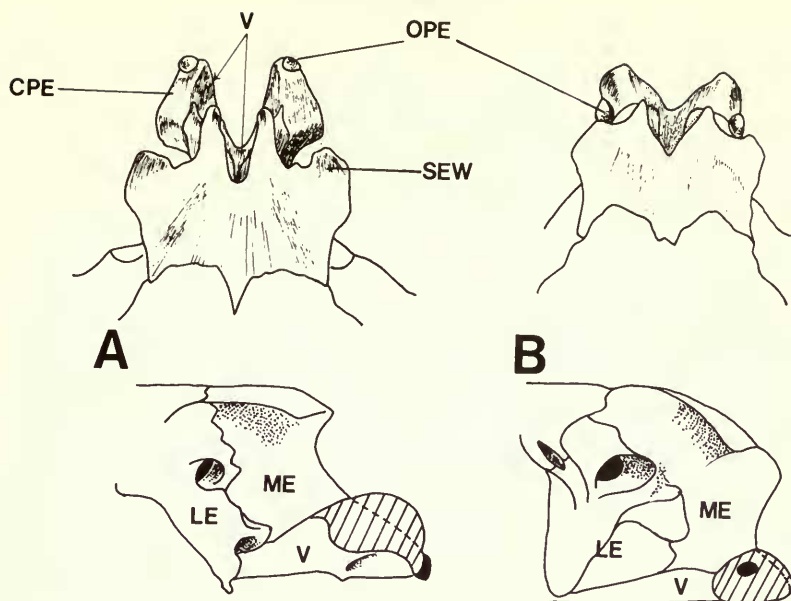


Fig. 5 Ethmo-vomerine regions in dorsal and lateral views: A. *Abramis brama*; B. *Xenocypris argenteus*. The lateral views are semi-diagrammatic and show the anterior edge of the vomer as a dashed line, the cartilaginous preethmoid as cross-hatched and the ossified preethmoid as black. Composites, from skeletal and alizarin specimens; all drawn to same scale.

well forward, the lateral ethmoids remain in medial contact. However, in *Barbus barbus*, *Cyprinus* and *Carassius*, the myodome invades the mesethmoid cartilage through a parting between the lateral ethmoids. Patterson (1975) was unable to conclude whether the absence of an anterior myodome was a primitive condition or due to secondary loss (apomorphic). Its presence does not seem necessarily to be correlated with any particular degree of ethmoidal elongation, nor its absence with any shortening. In noemacheilids, gobiinids and catostomids, an anterior myodome is lacking. Widespread, mosaic distribution in cyprinids and almost universal presence in characoids probably indicates that an anterior myodome is a plesiomorph feature.

In *Ctenopharyngodon* and *Mylopharyngodon* the olfactory foramen is entirely counter-sunk within the lateral ethmoid, whereas in *Hypophthalmichthys* it projects forward as a bony tube (Fig. 4). In the latter genus there is a tubular opening between the medial dorsal part of the lateral ethmoid wall and the overlying frontal (LEF, Fig. 4). This tube contains a thick ligament which covers the top of the lateral ethmoid wall and the outer part of the supraorbital. A similar feature occurs in *Xenocypris* (Fig. 5B). In cyprinids the olfactory foramen is most often formed from the anterior margin of the mesethmoid. In some taxa, however, the foramen is confined entirely within the lateral ethmoid. This occurs in the taxa cited above, in alburnine genera (*Alburnus*, *Chalcalburnus*) and some *Barbus*. In *Barbus tropidolepis* the foramen is also housed in an anteriorly projecting tube (Banister, pers. comm.). On the basis of other sets of synapomorphic characters it is hypothesized that the occurrence of a tubular olfactory foramen in diverse taxa is of no phyletic significance.

A short and broad vomer is hypothesized as plesiomorphic eg. as in *Ctenopharyngodon* and *Hypophthalmichthys*. However, in *Hypophthalmichthys* the vomer extends anteriorly to floor the median ethmoid notch, its anterior margin is almost straight and is curved upward so as to face the lower part of the ethmoid bloc. Laterally, the vomer is indented to contain the preethmoid. An anteriorly extended vomer, flooring the median ethmoid notch is a rarely encountered feature amongst cyprinids. In some cultrines (*Culter*) and in *Ochetobius* (currently included in the Leuciscinae), the vomer forms the floor of a shallow but wide

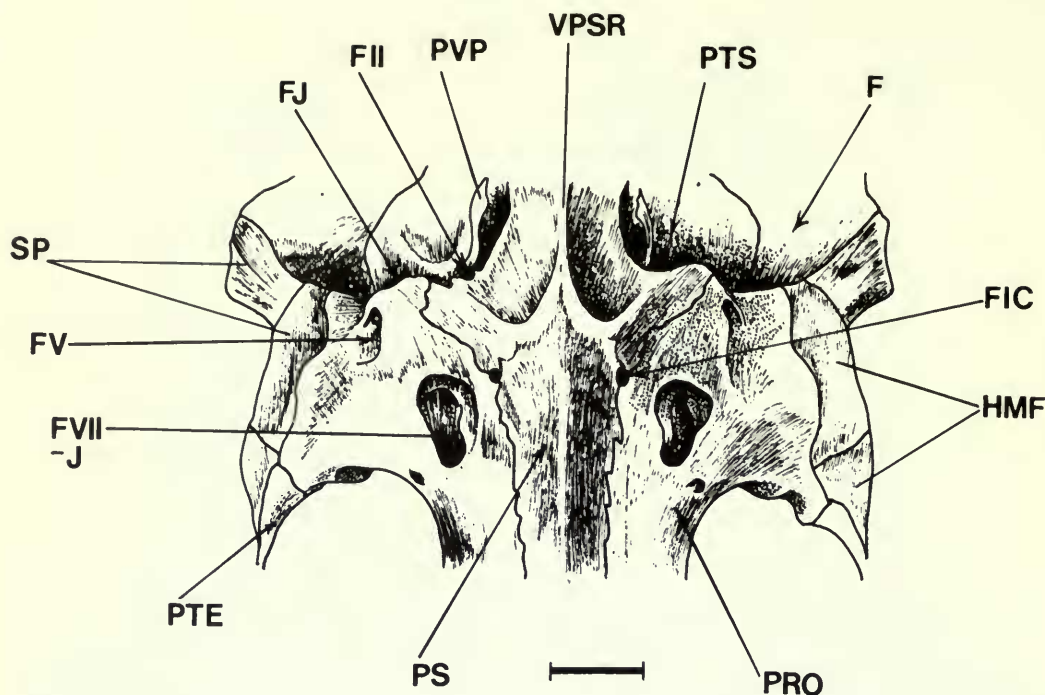


Fig. 6 *Ctenopharyngodon idellus*, ventral view of anterior otic region. Specimen BMNH 1888.5.15 : 25. Scale = 10 mm.

ethmoid notch. In *Xenocypris* and *Abramis*, the vomer also floors the ethmoid notch but the mesethmoidal walls are deep, almost meeting one another ventrally and leaving only a narrow area of the vomerine floor visible from above (Figs 5A & B). As mentioned above (p. 7) *Xenocypris*, *Abramis*, *Chondrostoma* and *Rutilus* differ from other cyprinids in employing the vomer as the platform for the preethmoid and excluding the mesethmoid from taking part in its support. In these genera the vomer is deeply forked, each arm extending some distance anteriorly from the mesethmoidal border; in transverse plane the bone is markedly convex.

2. Pterosphenoid

Ctenopharyngodon (Fig. 6); contact between the pterosphenoid and ascending process of the parasphenoid is *via* a thin strut; medial contact with the prootic is by a long suture. On the lateral face of the pterosphenoid is a small, ventrally directed process (autapomorphic feature; PVP, Fig. 6).

Hypophthalmichthys (Fig. 7); contact with the parasphenoid is *via* a thick, anteriorly directed pillar-like process. The part to the anterior trigemino-facialis foramen, and a medial portion of the bone provides the inner wall of the anterior part of the chamber; this is a unique condition in cyprinids.

Howes (1979) presented a classification of the various types of contact between the parasphenoid and pterosphenoid, assuming that this classification reflected a phylogenetic sequence for the Cyprinidae as a whole. Further analysis has shown that similar sequential series can be detected in all groups so far identified as monophyletic, i.e. the plesiomorphic condition is one with no contact between para- and pterosphenoid (Type 1 and derived Type 1 in Howes, 1980) and the most apomorphic condition involves extensive lateral contact between the pterosphenoid and parasphenoid (Type 5 in Howes, 1980).

A pterosphenoid pedicle is present in various teleosts and may or may not contact the

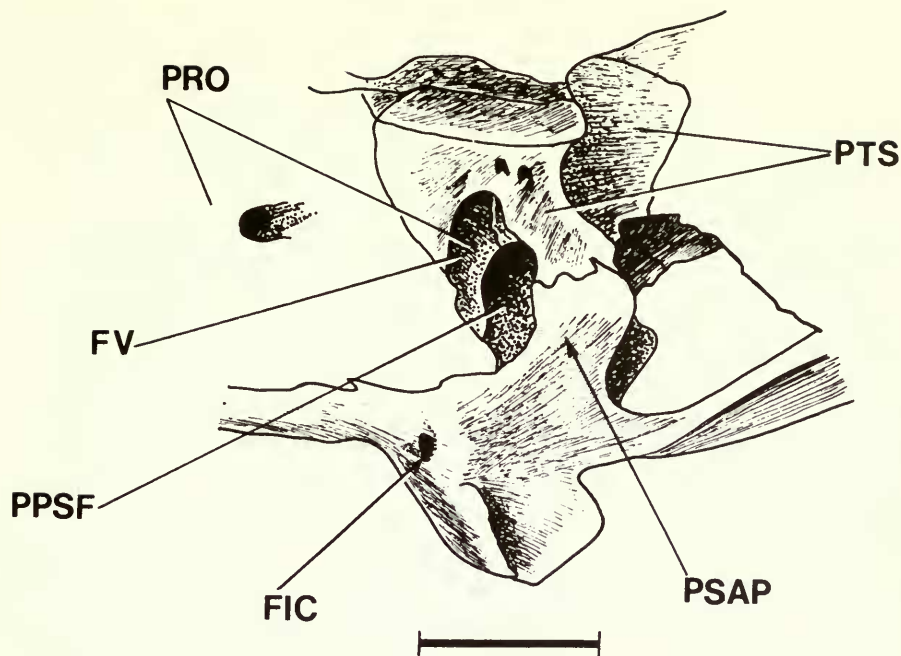


Fig. 7 *Hypophthalmichthys molitrix*, lateral aspect of anterior otic region, viewed slightly antero-ventrally. Drawn from specimen BMNH 1895.5.31 : 22 with additions from alizarin preparations and dissections from BMNH 1980.5.21 : 5-14. Scale = 10 mm.

parasphenoid ascending process. Patterson (1975) regards this feature as a plesiomorphic one.

3. Parasphenoid

In both *Ctenopharyngodon* and *Hypophthalmichthys* the parasphenoid is anteriorly broad, narrowing posteriorly in *Hypophthalmichthys* but remaining broad in *Ctenopharyngodon* in which genus it bears a marked ventral medial ridge. In *Hypophthalmichthys* the hypophyseal portion of the parasphenoid is ventrally extended into a long deep process, or keel the posterior edge of which is developed into a transverse ridge. The ventral keel serves both as the anterior point of attachment for a medial cartilaginous insert dividing the forward part of epibranchial diverticula (p. 23) and as lateral sites of attachment for the *adductor arcus palatini* muscle (p. 37).

In the majority of cyprinids the central surface of the parasphenoid is grooved, rarely is there a midline ridge or process, and these features are regarded as derived. The anterior broadening of the parasphenoid, although extreme in the Chinese major carps, is a common feature in cyprinids (see Ramaswami, 1955b). Weisel (1960) notes that in *Catostomus* the anterior part of the parasphenoid is considerably wider than that of cyprinids. However, this is not so when compared with the two taxa discussed here.

Ctenopharyngodon shares with *Mylopharyngodon* the developed ventral midline ridge and deep anterior concavity of the parasphenoid, both features regarded as apomorphic. The hypophyseal keel of *Hypophthalmichthys* is a feature shared with *Xenocypris* and *Abramis*, although in these taxa it is developed to a lesser extent (see below).

The *internal carotid fenestra* in *Ctenopharyngodon* is small and indents the posterior border of the parasphenoid ascending process and the antero-ventral margin of the prootic. In *Hypophthalmichthys* the internal carotid artery passes through a small foramen situated in the basal part of the parasphenoid keel (Fig. 7).

Patterson (1975) considered that the plesiomorphic condition of the carotid opening in

teleosts is for it to occur as a foramen within the parasphenoid. In nearly all cyprinids I have examined, and in all characoids, the internal carotid passes through a fenestra between the parasphenoid and the prootic, a condition Patterson (1975) thought derived and due to the eroding of the parasphenoid ascending process. In catostomids (see Weisel, 1960) and siluroids (?all) the foramen is situated entirely within the parasphenoid. Although similarly there is a parasphenoid carotid foramen in *Hypophthalmichthys* I consider this to be a derived condition in this taxon and for the following reasons.

In *Alburnus*, *Rutilus*, *Chondrostoma* and *Abramis*, the internal carotid fenestra is extensive (Fig. 8); it is covered laterally by a fascia of tissue and plugged by a wedge of fat leaving a small ventral opening to allow passage of the carotid vessel. In *Abramis* there is a tendency for the fenestra to elongate and in *Abramis sapa* the 'fenestra' is divided; the lower opening being confined to the parasphenoid and carrying the internal carotid artery, the upper indenting the ventral margin of the prootic and not providing passage for any vessel (Fig. 8). It is hypothesized that the condition of the carotid fenestra in *Abramis sapa* is a derived one and represents a transitional stage toward that in *Hypophthalmichthys*. That this is the directional path and not the reverse, viz the incorporation of the foramen into a fenestra, as indicated by the morphology of the parasphenoid. In *Abramis* there is a ventral extension of the hypophyseal part of the parasphenoid similar to that in *Hypophthalmichthys* (see above), and this is most highly developed in *A. sapa* (Fig. 8). Furthermore, the carotid foramen in *Hypophthalmichthys* is situated in the ventral keel, rather than (plesiomorphically) in the ascending process (Patterson, 1975). Similarly, an internal carotid foramen occurs in the same position in *Xenocypris* but is a larger hole than in *Hypophthalmichthys*.

On the basis of this evidence I suggest that the foramen for the internal carotid artery in *Hypophthalmichthys* and *Xenocypris* is secondarily derived in its position in the parasphenoid. This positioning has come about both as a consequence of the ventral prolongation of the parasphenoid and the re-orientation of the first branchial arch (p. 31) whereby the plane of the efferent artery would be sagittal rather than transverse. Thus, this shared feature in *Hypophthalmichthys* and *Xenocypris* is considered a synapomorphic character.

Modifications to the ventral border of the parasphenoid are present in a unit of leuciscine taxa represented by *Abramis*, *Rutilus* and *Chondrostoma*. In these genera, there is a deep ventral channel in the posterior part of the parasphenoid. The channel is confluent with a similar feature in the basioccipital and the whole is filled with a cartilaginous block (Fig. 27). Discussion of this character is reserved for inclusion with that of the basioccipital (p. 23).

Mention should be made here of medial parasphenoid processes. In *Labeo* and related taxa (see Howes, 1980 : 152, fig. 26 and p. 16 below) a process arises from either side of the medial wall of the parasphenoid just anterior to the optic foramen. Each process contacts the ventral border of each respective pterosphenoid. These medial processes vary from thin struts to thick pillars. Only in *Pelecus* is there a single, medial parasphenoid pillar. These structures are not to be interpreted as homologues of the basisphenoid. Harrington (1955) reported that Holmgren & Stensio (1936) recognized a basisphenoid in some cyprinids, eg. *Abramis*. However, the structure reported by Holmgren & Stensio is the lateral pterosphenoid strut that makes contact with the parasphenoid wing. The medial parasphenoid extensions of *Pelecus* and *Labeo* are considered as neomorphs.

4. Prootic

Ctenopharyngodon (Fig. 6); contact with the parasphenoid ascending process is via a long suture. The posterior opening of the trigemino-facialis chamber is large and lies ventrally. The upper posterior part of the bone is deeply concave and forms the entire inner face and part of the roof of the subtemporal fossa.

Hypophthalmichthys (Fig. 7); no contact with the parasphenoid ascending process. The posterior trigemino-facialis foramen is small and situated laterally. The upper posterior half

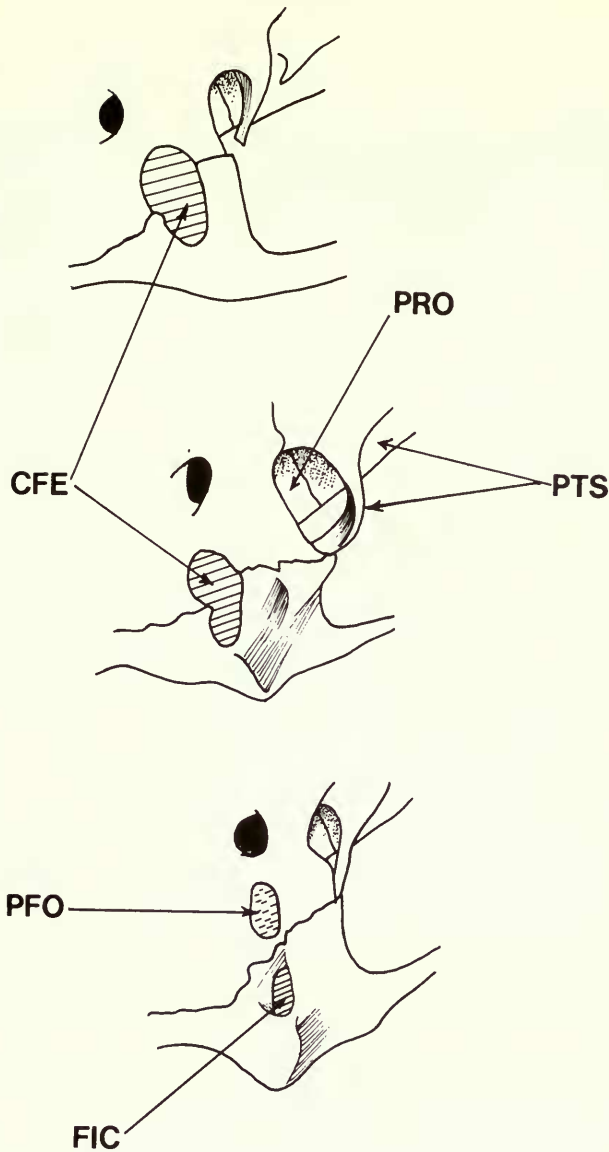


Fig. 8 Lateral views of anterior otic regions: (top) *Rutilus rutilus*; (centre) *Abramis brama*; (bottom) *Abramis sapa*. Semi-diagrammatic, compiled from several specimens.

of the bone is slightly concave and forms only the lower inner face of the subtemporal fossa. The lower part of the anterior border forms the posterior rim of the trigeminal exit fenestra.

The plesiomorphic condition of the prootic in cyprinids is hypothesized as an almost square bone, its lateral face hardly depressed, its anterior border interrupted by the trigeminal exit foramen and with a short lateral commissure (see for example, *Opsariichthys* in Howes, 1980). Derived conditions are those where the anterior trigeminal foramen pierces the lateral face; the lateral commissure is long, and the prootic contributes a ventral portion to the apophyseal platform.

The general depression of the otic part of the cranium in *Ctenopharyngodon* has resulted in the forepart of the prootic being laterally extended (Fig. 6), which, as a consequence, has shifted the orientation of the posterior trigeminal foramen. This opening faces ventrally

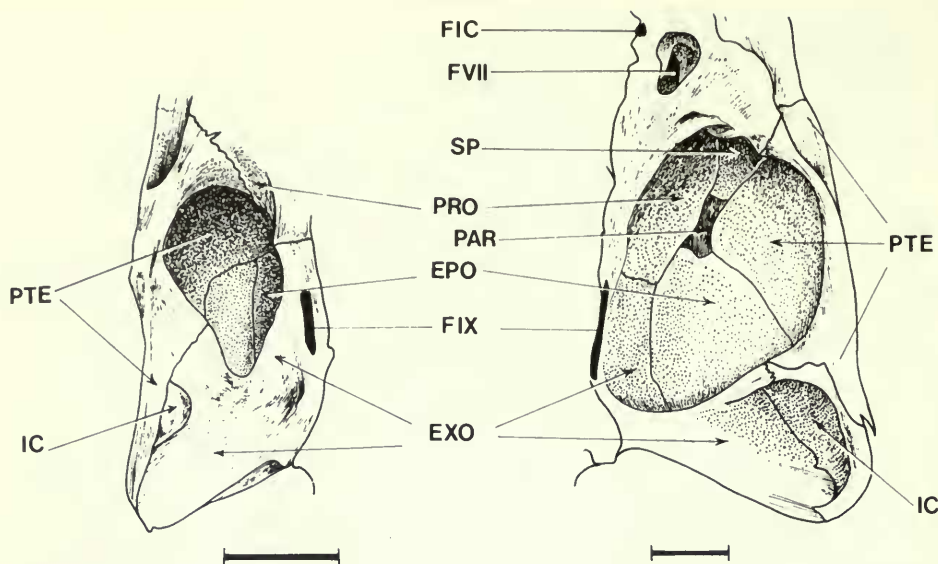


Fig. 9 Subtemporal fossae: (left) *Hypophthalmichthys*; (right) *Ctenopharyngodon*. Specimens BMNH 1888.5.31 : 22 and 1888.5.15 : 25. Scales = 10 mm.

instead of laterally, so the nerve trunk and jugular vein enter without passing across the prootic face. This derived condition occurs also in *Mylopharyngodon* and *Squaliobarbus*.

The most outstanding feature of the prootic in *Hypophthalmichthys* is the exclusion from the bone of the anterior trigeminal foramen. Only the lower part of the prootic forms the border of the opening, the upper part of the foramen being confined to the pterosphenoid. In one specimen, the upper part of the foramen, through which mdV and mxV exit is, on one side of the cranium, entirely enclosed in the pterosphenoid. Reduction of the anterior part of the prootic in *Hypophthalmichthys* appears to have occurred with the posterior movement of the pterosphenoid, itself associated with hypertrophy of the *adductor hyomandibularis* muscle. The form of the prootic in *Hypophthalmichthys* is an autapomorphic feature.

5. Subtemporal fossa

Ctenopharyngodon (Fig. 9); extensive, hemiovoid with a deep conical anterior portion, or chamber, that extends into the autosphenotic; the *levator posterior* muscle arising from that bone. The inner wall of the fossa is formed from the prootic, the roof from the pterotic and epioccipital, and anteriorly from the sphenotic. None of these bones meet dorsally and the ventral surface of the parietal is exposed thus also contributing to the subtemporal fossa roof.

Hypophthalmichthys (Fig. 9); almost pyramidal, lacking an anterior sphenotic extension. The posterior, exoccipital border of the fossa is indented by a notch. The bones forming the inner wall of the fossa, prootic, exoccipital and epioccipital, do not meet along their respective dorsal and anterior borders, the space between being a thin cartilage wall.

The most frequently occurring subtemporal fossa morphology amongst the Cyprinidae is one which is deep and circular or ovate. The fossa is the site of origin for *levator posterior* muscles running to the pharyngeal bone and its size is correlated with that of the muscles' size and their orientation. It is thus difficult to assess the polarity of some features such as the posterior notch, which occurs not only in *Hypophthalmichthys* but in a variety of 'leuciscine' and 'barbine' taxa. There is generally a space between the bones forming the inner wall of the subtemporal fossa (*viz* between the posterior-dorsal edge of the prootic, posterior edge of the sphenotic, and antero-dorsal edge of the epioccipital) across which is a thin cartilage and which forms the apex of the fossa. In this feature *Ctenopharyngodon* and *Hypophthalmichthys* are each autapomorphic. In the former taxon the space is covered by the parietal

and in the latter taxon the exoccipital contributes substantially to the inner face and its antero-dorsal edge contacts the cartilaginous sheet.

The vast subtemporal fossa of *Ctenopharyngodon* is a feature shared only with *Mylopharyngodon* and *Squaliobarbus*. Likewise, in these two genera the fossa extends anteriorly deep into the sphenotic from which the *levator posterior* musculature originates. The size, shape and sphenotic contribution of the subtemporal fossa in these three genera is considered synapomorphic. The anterior contribution of the sphenotic to the subtemporal fossa occurs also to a greater or lesser degree in *Cyprinus*, *Carassius* and in some *Barbus*, and in the two former taxa part of the *levator posterior* musculature originates in that anterior extension. This may thus represent a synapomorphy linking all these genera (see p. 49).

The shape and depth of the *Hypophthalmichthys* subtemporal fossa are shared with *Xenocypris*. However, these parameters are treated with caution as synapomorphies; variations in subtemporal fossa depth cover a wide range throughout the cyprinids. *Abramis* has what is possibly the deepest subtemporal fossa and again, its pyramidal shape greatly resembles that of *Hypophthalmichthys*. Neither in *Xenocypris* nor *Abramis* does the exoccipital contribute substantially to the inner wall of the subtemporal fossa. Only in *Rutilus* does the anterior edge of the exoccipital penetrate forward so as to separate the prootic and epioccipital.

6. Dilatator fossa

Ctenopharyngodon (Fig. 10); formed mostly from the sphenotic which extends laterally with a small anterior contribution from the frontal; the frontal border forms a medial roof to the fossa.

Hypophthalmichthys (Fig. 10); formed in almost equal parts from the frontal and sphenotic and sloped antero-laterally as a broad shelf.

The plesiomorph condition of the dilatator fossa in cyprinids is considered to be one in which the fossa is small and formed from nearly equal portions of the frontal, sphenotic and pterotic, and to be roofed or partially roofed by the frontal. This type of fossa morphology is widespread amongst cyprinids and is represented in *Ctenopharyngodon*. An almost identical type of dilatator fossa morphology in characoids is regarded by Vari (1979) as plesiomorphic. In siluroids there is no cranial fossa, the *dilatator operculi* muscle originating from the ventral cranial surface (see Alexander, 1964). Similar ventral muscle origin is to be found in some cyprinids and characoids (see below; Alexander, 1964; Howes, 1978). In most catostomids the dilatator fossa is well developed and involves the sphenotic and the medial part of the frontal. Cobitids (*sensu lato*) possess a small fossa of the type which involves mostly the sphenotic.

It would seem that from the plesiomorphic type of dilatator fossa two avenues of development were open. One was toward extended coverage of the cranial roof, involving mostly the frontal. The second was for the frontal to become invaginated ventro-medially and be pierced by the *dilatator operculi*. The most derived state of the first morphotype in cyprinids is that in *Hypophthalmichthys* where the major contributing elements to the fossa are the frontal and sphenotic, the pterotic being virtually excluded. The sphenotic extends laterally as a broad, ventrally sloping shelf confluent with the frontal. The lateral part of the frontal also slopes and medially bears a ridge which forms the border of the fossa. A similar form of dilatator fossa occurs in *Xenocypris* and *Abramis*, but in these genera the frontal and sphenotic have a more acute ventral slope.

The most derived state of the second morphotype is that where a divided *dilatator operculi* muscle passes through a frontal foramen and a fenestra between the frontal and sphenotic (see below).

These two morphotypes embrace the four enumerated by Howes (1978). Type 1 is described above as the plesiomorph condition and Types 2 and 3 are morphoclinical stages in the encroachment of the cranial surface.

Within the second lineage (Type 4 of Howes, 1978), in which the *dilatator operculi*

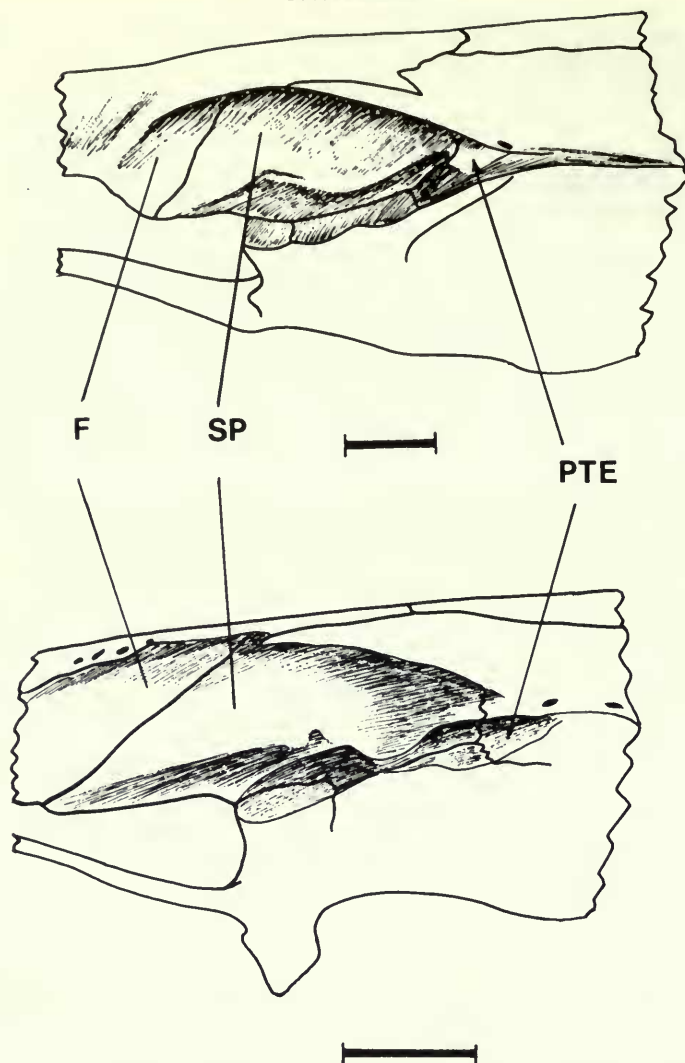


Fig. 10 Dilatator fossae: (upper) *Ctenopharyngodon*; (lower) *Hypophthalmichthys*. Scales = 5 mm. Specimens as previous figure.

originates from the ventral surface of the frontal, a possible transitional sequence can be distinguished. An early stage is hypothesized as being represented by *Squaliobarbus*. Here the frontal is deeply indented anteriorly to the sphenotic and contains a small foramen which enters the orbital cavity. In *Barbus* and *Capoeta* the muscle has 'broken through' the frontal to attach to its ventral surface inside the orbital cavity. A previous statement (Howes, 1978) to the effect that the frontal and sphenotic in *Barbus* contacted each other only along their lateral margins is incorrect. The anterior margin of the sphenotic is bordered by the frontal, albeit in some instances an extremely thin segment (Fig. 11). *Carassius* and *Cyprinus* appear to mark a further stage in development of the foramen for there is in some specimens an almost complete separation between the frontal and sphenotic, the ventro-lateral part of the frontal extending only part way along the sphenotic margin. *Cyprinus* is the more derived taxon in this respect since it has an almost complete frontal-sphenotic foramen (Fig. 11). *Labeo* and *Garra* appear to represent the most derived state, with the *dilatator operculi* being divided, the upper section passing through a frontal foramen, the lower through a foramen between the frontal and a strut-like sphenotic process (Fig. 11). The doubly foraminate forms

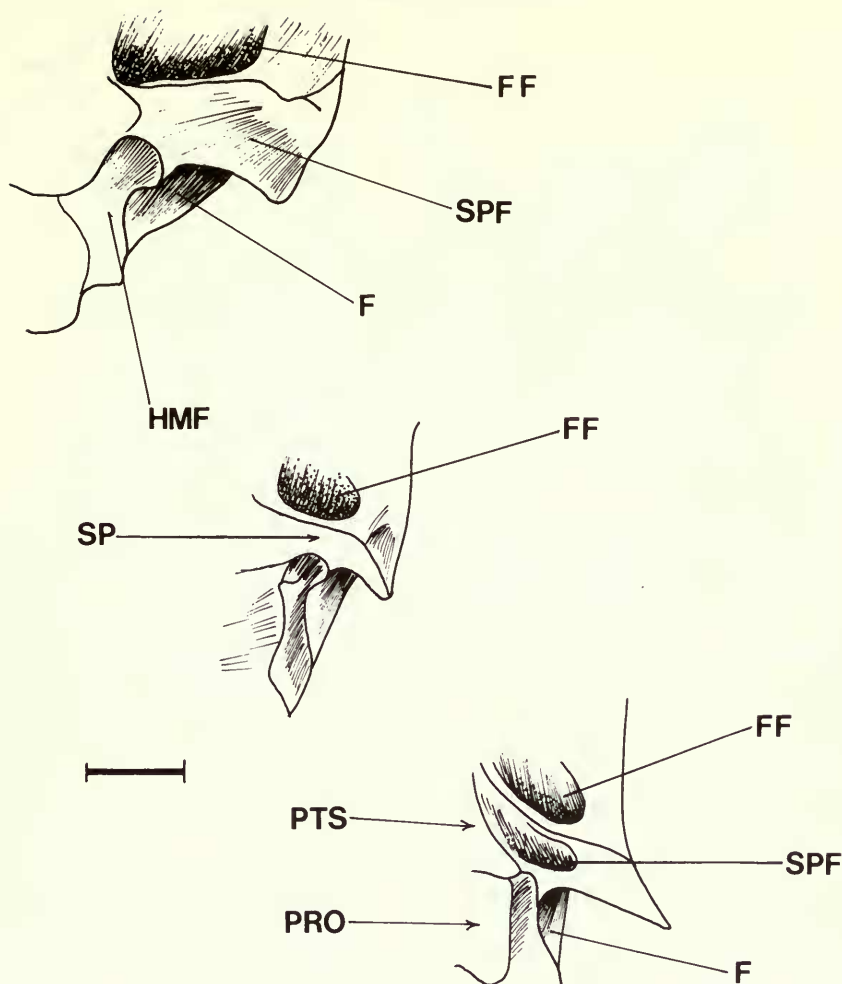


Fig. 11 Dilator fossae: (upper) *Cyprinus carpio* (uncatalogued); (centre) *Capoeta capoeta* BMNH 1879.11.14 : 19; (lower) *Labeo coubie* BMNH 1907.12.2 : 3744.

of dilatator channel appear to be rewarding characters for the classification of those taxa in which they occur and work in preparation discusses the feature in more detail (Banister & Howes, in preparation).

7. Frontal

Ctenopharyngodon (Fig. 12); broad and short, forming 50% of the cranial length (anterior tip of the ethmoid to the posterior border of the parietal), 5–6 pores in the embedded sensory canal, lateral part sloping ventrally at 27° to the transverse plane, a triangular depression occurs above the supraorbital.

Hypophthalmichthys (Fig. 12); broad anteriorly, narrow posteriorly, forming 75% of the cranial length; anterior lateral part sloped ventrally at 45° ; sensory canal is an osseous tube on the surface, with 9–10 pores.

In cyprinids, the plesiomorph condition of the frontal is considered to be short and broad (Howes, 1978 : 31). Only in derived members of monophyletic lineages are the frontals elongate, with an increased number of sensory pores. The raised tubular sensory canal, as in *Hypophthalmichthys*, is a feature Tretiakov (1946) used in marking *Tinca* as a primitive cyprinid related to catostomids—which also possess this character. However, in catostomids

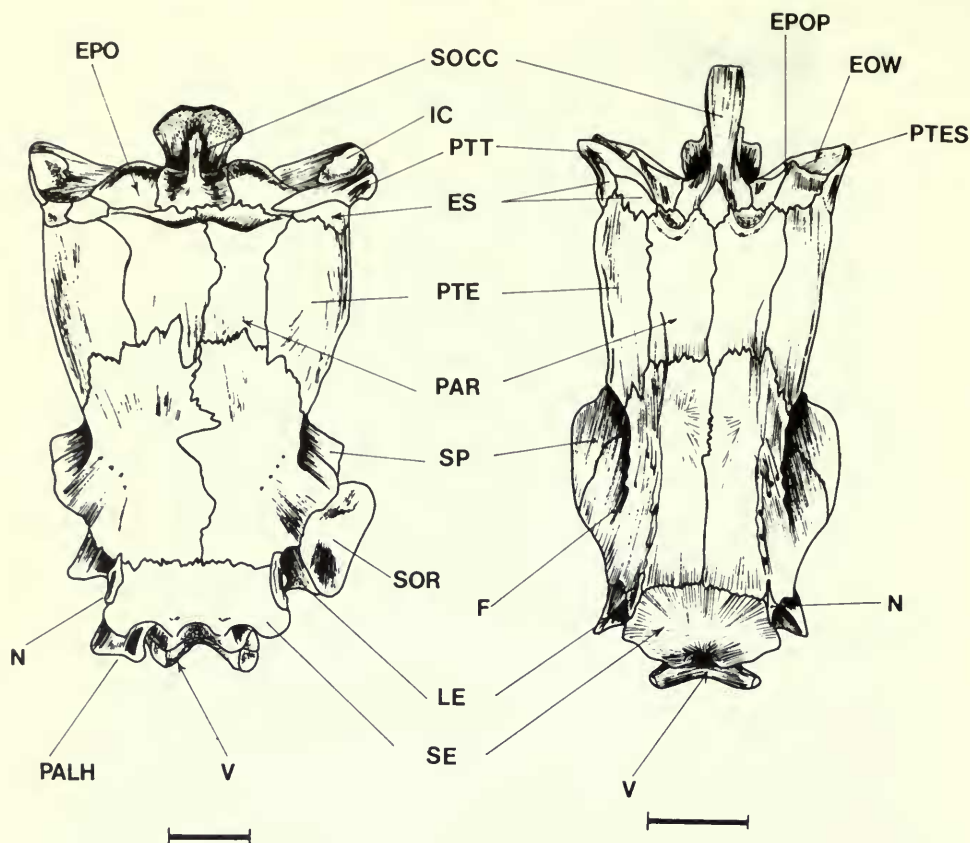


Fig. 12 Dorsocrania: (left) *Ctenopharyngodon*; (right) *Hypophthalmichthys*. Scales = 20 mm. Specimens as previous figures.

the situation is rather different for here the canal is mostly detached from the frontal and runs at the surface of thick subcutaneous tissue covering the cranium (see comments by Sagemahl, 1891 : 508 and Weisel, 1960 : 122). Although raised frontal canals are an uncommon feature in Cyprinidae they occur in abramine genera (see p. 45 for included genera), some cultrines and some chelines (eg. *Oxygaster*). This pattern of ossification has possibly been derived independently in these several groups.

The frontal morphology in *Ctenopharyngodon* is generally of the plesiomorphic type but sloped and laterally depressed, extended border of the bone is a derived state and shared with *Mylopharyngodon*. The markedly sloped frontal in *Hypophthalmichthys* is shared only with *Xenocypris* and *Abramis*.

8. Parietal

Ctenopharyngodon (Fig. 12); as broad as the frontal and half its length.

Hypophthalmichthys (Fig. 12); half the greatest width of the frontal and 65% of its length.

Commonly in cyprinids, the parietal is short, being 30%–50% of the frontal length. A parietal fontanelle is usually absent in Cyprinidae but may be found in specimens of *Cyprinus* and various gobioides (see Ramaswami, 1955a). This feature, widespread in other otophysans is possibly a plesiomorph character and closure of the fronto-parietal fontanelle is to be regarded as apomorphic for the Cyprinidae (see also Fink & Fink, 1981).

9. Circumorbital bones

Ctenopharyngodon (Fig. 13); 1st infraorbital thick and curved outward, 2nd and 3rd

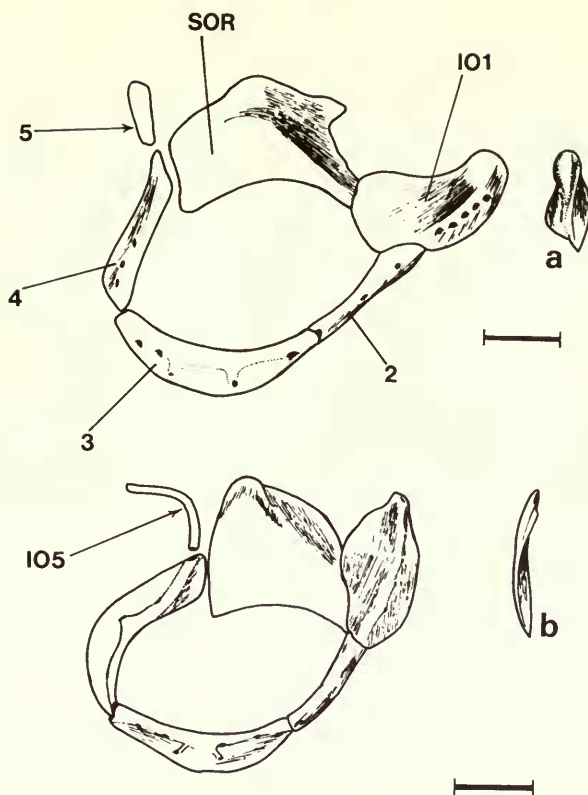


Fig. 13 Circumorbital bones: (upper) *Ctenopharyngodon*; (lower) *Hypophthalmichthys*. a and b are anterior views of the respective 1st infraorbitals. Scales = 10 mm.

infraorbitals elongate, 4th almost perpendicular, 5th long, crossing the sphenotic; supra-orbital extensive.

Hypophthalmichthys (Fig. 13); 1st infraorbital thin, vertically aligned; 2nd, 3rd and 4th elongate, 5th, an almost right-angled bone, the vertical portion crossing the frontal, the horizontal part across the sphenotic; supraorbital extensive.

In both genera the supraorbital is extensive and has the effect of extending ventrally the lateral border of the cranial roof so that the ventral edge of the supraorbital comes to lie in the same horizontal plane as that of the parasphenoid. In *Ctenopharyngodon* the supra-orbital slopes laterally at the same angle as the frontal, its medial portion is thickened and anteriorly bears a wide groove. The lower anterior border of the bone contacts the postero-dorsal edge of the 1st infraorbital. In *Hypophthalmichthys* the supraorbital is directed almost perpendicularly and its anterior part contacts half the dorsal margin of the 1st infraorbital. In small specimens (up to 100 mm SL), only the canal tube of infraorbitals 2–5 is ossified, the upper part of the 4th being fragmented into as many as four portions (Fig. 14).

Comments made previously concerning infraorbitals (Howes, 1978; 1980) suggested that both extreme reduction and expansion of the elements could be seen as derived states. Of these the most often encountered condition in cyprinids is for there to be a reduction of infraorbital ossification, particularly that of the 5th bone, and also this bone's dissociation from the supraorbital.

Gosline (1974) made much of the type of infraorbital-supraorbital sensory canal connection, dividing cyprinids into two groups on the basis of whether or not there was a continuous connection between the two canal systems. Howes (1978) refuted this suggestion by noting that there was always some kind of connection between the canals. What is

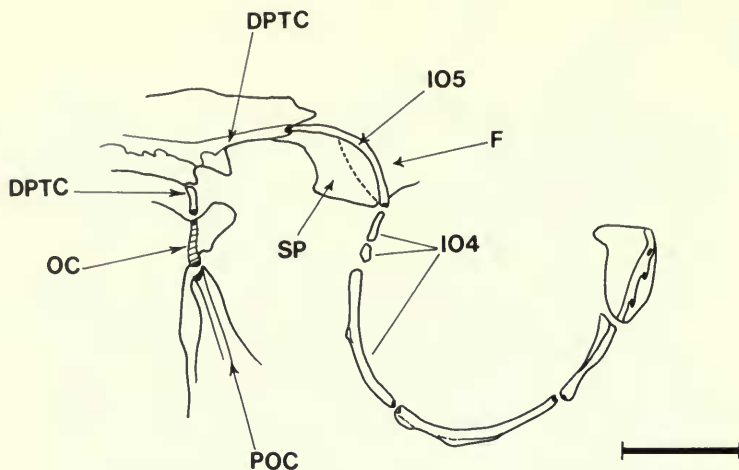


Fig. 14 Circumorbital bones and opercular-pterotic canal system of *Hypophthalmichthys molitrix*. Drawn from an alizarin specimen 65 mm SL. Scale = 3 mm.

possibly of more significance is the form of the 5th infraorbital and its association with the dermosphenotic. Contrary to a previous statement (Howes, 1978) the dermosphenotic is present in many cyprinids (the element labelled as a dermosphenotic in *Oreoleuciscus* [Howes, 1978, fig. 22] appears to be the fragmented 5th infraorbital, and that in '*Chelaethiops*' [Fig. 23] part of the dermopterotic). The distribution of the dermosphenotic amongst cyprinids and the morphology of associated canal systems is discussed in a separate paper (Banister & Howes, in preparation).

The thickened 1st infraorbital of *Ctenopharyngodon* is an autapomorphic feature, although there is a tendency towards thickening of that bone in *Mylopharyngodon*. Both genera, however, share the derived, massive ridged supraorbital. Similarly, the enlarged supraorbital of *Hypophthalmichthys* is shared with *Xenocypris*. But, again the infraorbital pattern of *Hypophthalmichthys* is autapomorphic.

10. Supraoccipital

Ctenopharyngodon (Fig. 12); short with posterior lamellate process.

Hypophthalmichthys (Fig. 12); long with dorsally thickened crest.

The supraoccipital of *Ctenopharyngodon* is the type most commonly present in Cyprinidae viz an almost square bone with a low crest. The broad, thick supraoccipital crest of *Hypophthalmichthys* is not encountered elsewhere in the cyprinids. Another autapomorphic feature occurring in this genus is that the anterior portion of the supraoccipital is on a raised platform, the sides of which are contributed by the parietals.

11. Exoccipital

Ctenopharyngodon (Fig. 15); contains a fossa posterior to the subtemporal fossa; the postero-ventral border of the bone is horizontal.

Hypophthalmichthys (Fig. 15); without supplementary fossa; postero-ventral border sloping laterally and caudally.

An earlier statement (Howes, 1978 : 38) claimed that in cyprinids the exoccipital showed little variability. This is not the case in the two genera now under discussion.

In *Ctenopharyngodon* the posterior border of the exoccipital lateral wall is horizontal—a condition considered plesiomorphic on account of its widespread distribution. The dorsal part of the bone, immediately posterior to the subtemporal fossa, bears a shallow depression (also contributed to by the intercalar—see below). From this supplementary fossa there arises a posterior section of the *levator posterior* muscle.

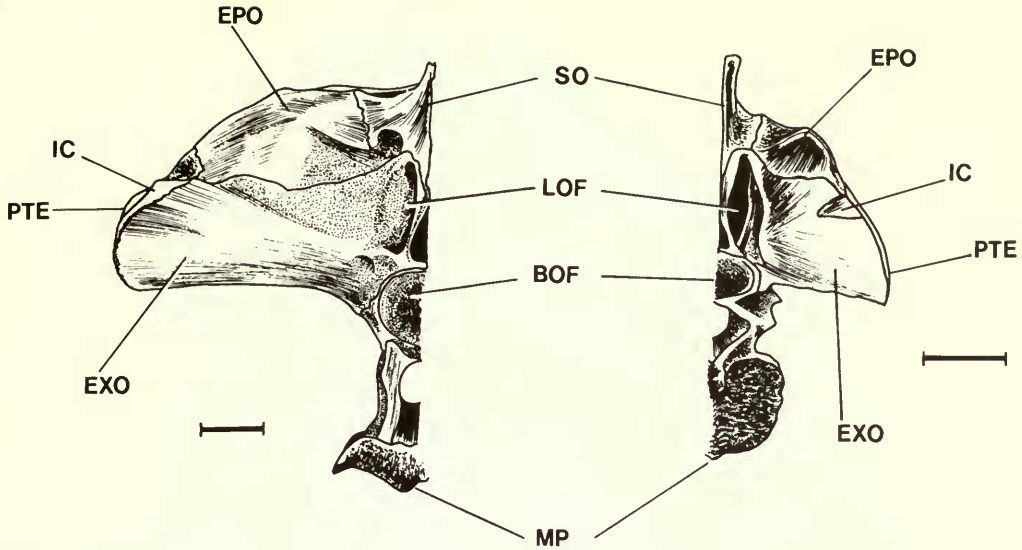


Fig. 15 Posterior cranial region: (left) *Ctenopharyngodon*; (right) *Hypophthalmichthys*. Scales = 10 mm. Specimens as previous figures.

In *Hypophthalmichthys* the posterior exoccipital wall slopes ventrally at an angle of 45° to the horizontal, its ventral border is also directed laterally at a similar angle with the result that the entire wall forms a triangular wing. The postero-lateral flaring of the exoccipital wall is so great that its distal edge contacts the distal tip of the pterotic spine—a feature otherwise present only in *Xenocypris*. In all other cyprinids examined the pterotic spine is separated from the exoccipital margin by a substantial part of the pterotic floor or by the intercalar. The dorsal surface posterior to the subtemporal fossa is flat, the *levator posterior* taking its origin entirely from the subtemporal fossa.

A *levator posterior* with a section originating from a supplementary subtemporal fossa as in *Ctenopharyngodon* is known elsewhere only in *Mylopharyngodon* and *Squaliobarbus* and is considered synapomorphic.

The *lateral occipital fenestra* in *Ctenopharyngodon* is narrow and when viewed posteriorly is obscured by the exoccipital medial border; a feature which otherwise occurs only in *Mylopharyngodon*. In contrast, there is an extensive fenestra in *Hypophthalmichthys*. In the Cyprinidae there is quite some variation in the size and shape of the fenestra although usually it is small and ovate. Rarely does it have the proportions of that in *Hypophthalmichthys*, which are approached only by *Xenocypris* and *Abramis*. To my knowledge, the fenestra is never reduced to the extent of *Ctenopharyngodon* and *Mylopharyngodon*. Both these conditions may be recognized as derived states.

12. Epioccipital

Ctenopharyngodon (Fig. 15); bullate with a slight posterior ridge; posttemporal fossa exists as a mere depression between the epioccipital and the pterotic.

Hypophthalmichthys (Fig. 15); triangular with a prominent posterior lip below which is a depression of the epioccipital wall; posttemporal fossa well-developed, extending somewhat anteriorly between the epioccipital and pterotic.

The epioccipital in *Ctenopharyngodon* is greatly developed and contributes the major part to the formation of the subtemporal fossa. As in all cyprinids the epioccipital roof provides the major site of origin for the *levator posterior* muscles (see Eastman, 1971). The bone in *Hypophthalmichthys* is virtually pyramidal and posteriorly has a broadly pointed lip. This lip or shelf serves for the attachment of hypaxial musculature and although variously developed throughout cyprinids in none is it more so than in this taxon.

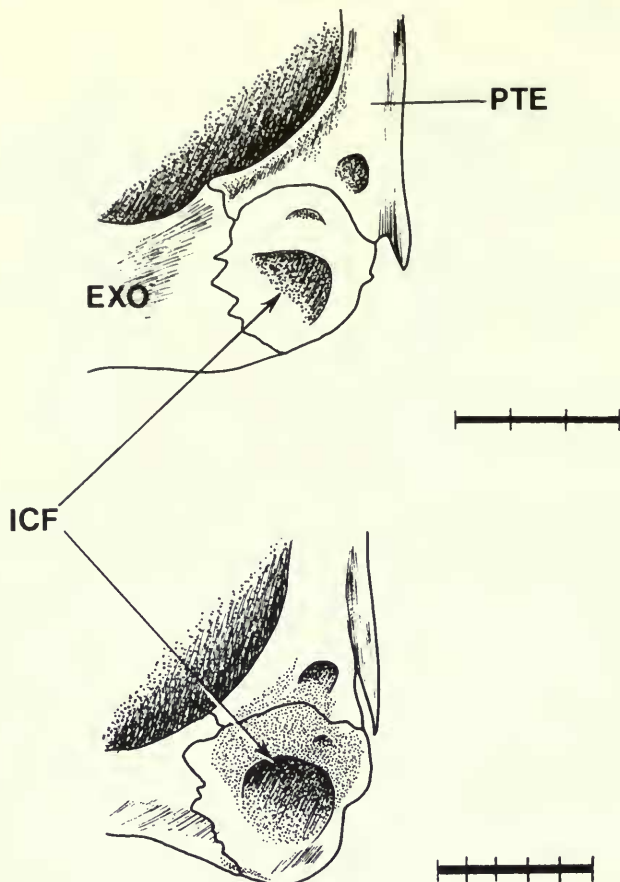


Fig. 16 Intercalar: (upper) *Squaliobarbus curriculus* BMNH 1888.5.15 : 29; (lower) *Mylopharyngodon piceus* BMNH 1895.5.31 : 40. Scales in mm divisions.

13. Intercalar

Ctenopharyngodon (Fig. 16); extensive and forming the posterior corner of the cranium between the basioccipital and pterotic. Its ventral surface contributes to the supplementary subtemporal fossa (see above) and provides the site of origin for the posterior section of the *levator posterior* muscle.

Hypophthalmichthys (Fig. 16); smaller than the former taxon, when viewed posteriorly is seen as a triangular wedge intruding into the lateral border of the exoccipital (Fig. 15). Its ventral surface is broad and lies between the exoccipital and medial edge of the pterotic spine (Fig. 9). The intercalar morphology of *Hypophthalmichthys* is autapomorphic.

In cyprinids the intercalar is transitory, as for example in the aspinine group (see Howes, 1978) where it is well-developed in most members, but absent in the more derived taxa. Rarely is the intercalar developed to the extent that it is in *Ctenopharyngodon* and occurs similarly only in *Mylopharyngodon* and *Squaliobarbus* (Fig. 16) where it also provides the site of origin for part of the *levator posterior* muscle.

In *Capoeta* the intercalar also contributes to the area of origin of the *levator externus* (Fig. 17). However, in this genus the intercalar forms the lateral border to the exoccipital. The posterior wall of the exoccipital is strongly concave and provides the site of origin for the remainder of the posterior segment of the *levator* muscle. The exoccipital wall is strongly concave and its lateral margin is separated by a wide gap from the pterotic spine. In *Cyprinus* and *Carassius* the posterior wall of the exoccipital is virtually identical to that of *Capoeta*.

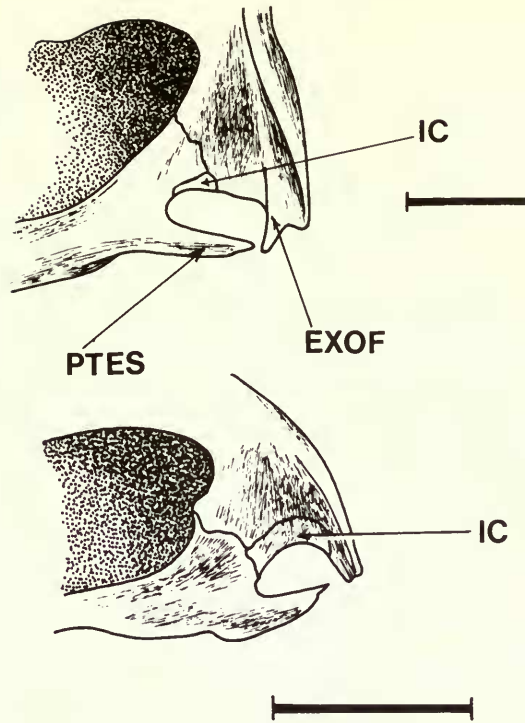


Fig. 17 Postero-ventral region of the cranium: (upper) *Cyprinus carpio* (uncatalogued); (lower) *Capoeta capoeta* BMNH 1879.11.14 : 19. Scales = 5 mm.

However, in these two genera, the intercalar is minute (or may even be absent) and is confined to the lateral edge of the pterotic; it plays no part in providing an area of attachment for the *levator posterior* muscle.

14. *Basioccipital*

Ctenopharyngodon (Fig. 19a); ventral keel shallow, concave anteriorly; masticatory plate large and ovate with a shallow ventral depression; pharyngeal pad thick, lozenge shaped with a longitudinally ridged surface; pharyngeal process broad and thick, its distal end rounded and upwardly curved; basioccipital facet circular.

Hypophthalmichthys (Figs 18a & 19e); ventral keel deep with markedly concave anterior border; masticatory plate cardiform, cancellous with a thick anteriorly directed point; pharyngeal pad thin, keratinized, its surface bearing a median ridge; pharyngeal process elongate, cylindrical and ventrally directed; basioccipital facet ovate.

Although there is quite some variation in the morphology of the basioccipital keel and its associated masticatory plate, that of *Hypophthalmichthys* is outstanding in its length and shape. Only in *Xenocypris* and *Distoechodon* is there a similar degree of development of the basioccipital keel (see illustrations in Tomodo, 1979 : 96). The ventral prolongation of the basioccipital in *Hypophthalmichthys* is associated with the epibranchial organs and serves for the attachment of the epibranchial duct and a medial ligament that stems from the cartilaginous bloc running along the midline. Genera which most closely approach *Hypophthalmichthys* and *Xenocypris* (including here *Distoechodon*) are *Rutilus* and *Chondrostoma* (Figs 18d & c). In these genera and *Abramis*, the ventral border of the basioccipital just anterior to the aortic foramen is formed into a deep channel. The most derived condition is in *Abramis* where a rounded notch indents the ventral border of the bone. The basioccipital channel is confluent with a similar feature of the parasphenoid (see p. 12) and is filled with cartilage.

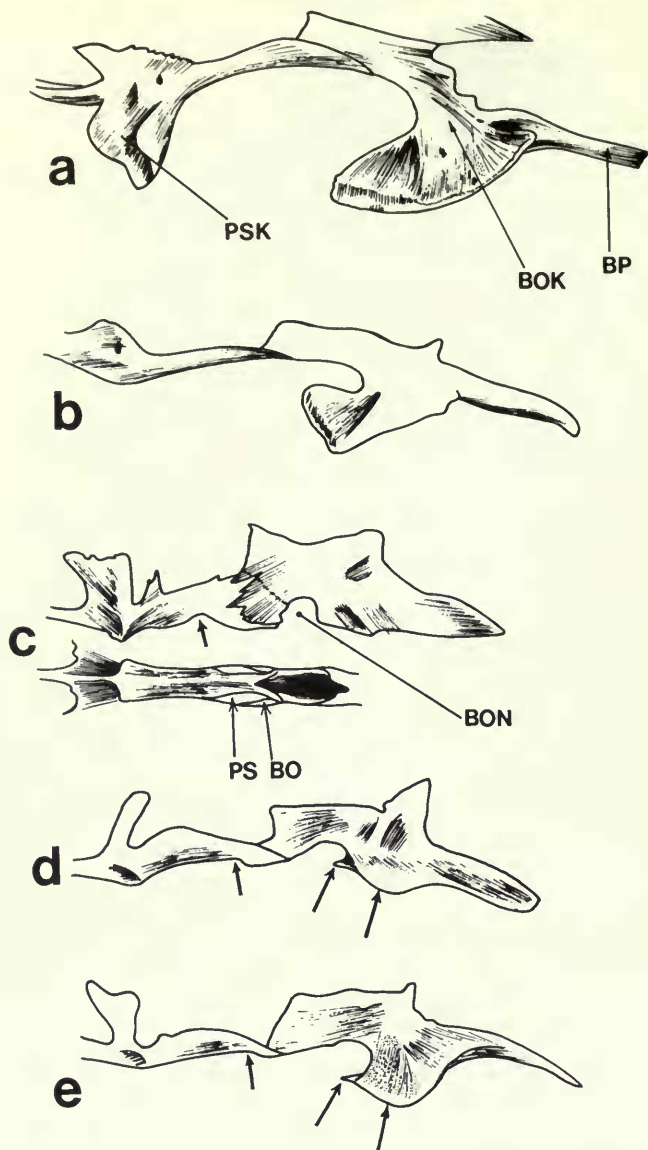


Fig. 18 Basicrania in lateral view: a. *Hypophthalmichthys molitrix*; b. *Xenocypris argenteus*; c. *Abramis brama*; d. *Rutilus rutilus*; e. *Chondrostoma nasus*. *Abramis* (c) is also shown in ventral view. The solid arrows indicate considered apomorphic features of the parasphenoid-basioccipital. Composites, all drawn to same scale.

The shape and size of the basioccipital masticatory plate is variable in the Cyprinidae. Being part of the pharyngeal feeding mechanism it would be expected that a particular pharyngeal dentition would be associated with a specific plate morphology. By and large this appears to be the case; the most common type of plate is a small triangular one with a compressed triangularly shaped posterior process. This morphology is associated with omnivorous or piscivorous dental types (simple, often single-rowed, recurved teeth). The pharyngeal plate of *Ctenopharyngodon* greatly resembles that of *Squaliobarbus* and *Rutilus* (Figs 19a, c & d), both regarded as being plesiomorphic. However, the posterior pharyngeal process is of a unique type whereas that in *Rutilus* and *Squaliobarbus* is of the plesiomorphic form. *Mylopharyngodon* exhibits a derived, bowl-shaped plate—associated with molariform

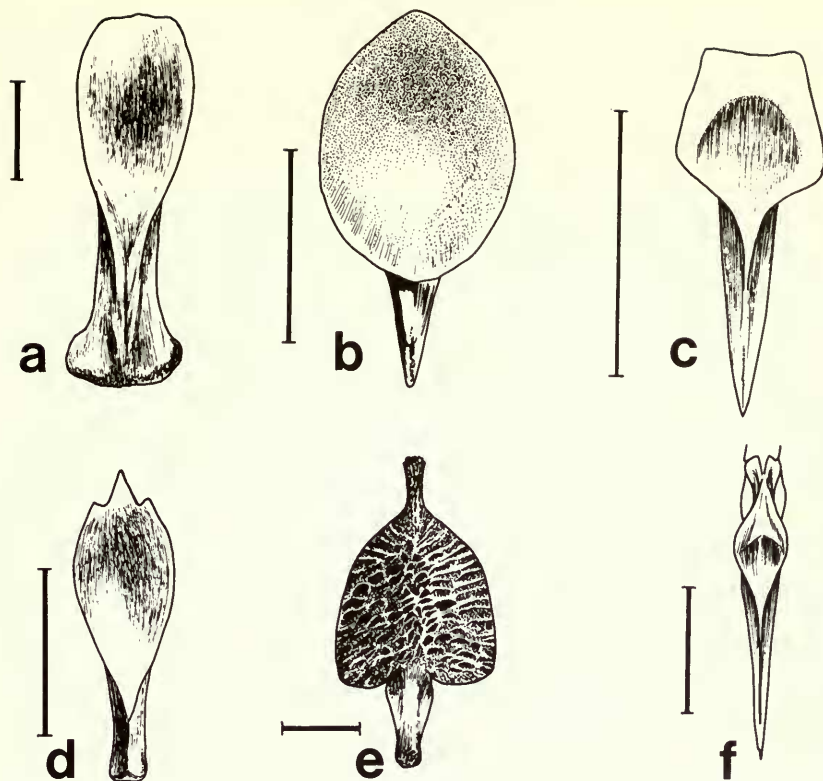


Fig. 19 Basioccipital masticatory plates: a. *Ctenopharyngodon idellus* BMNH 1888.5.15 : 25; b. *Mylopharyngodon piceus* BMNH 1895.5.31 : 40; c. *Squaliobarbus curriculus* BMNH 1888.5.15 : 29; d. *Rutilus rutilus* uncatalogued skeleton; e. *Hypophthalmichthys molitrix* BMNH 1895.5.31 : 22; f. *Abramis brama* uncatalogued skeleton. Scales = 10 mm.

dentition—but one obviously little modified from the plesiomorphic pattern and seemingly achieved by lateral and posterior expansion (Fig. 19b). A similarly developed plate type is found in *Labeo* species but here, the pharyngeal process is differently modified, forming a roof over the aortic channel (Reid, 1978, unpublished thesis). Another derived state occurs in *Abramis* where the pharyngeal plate has virtually disappeared (Fig. 19f). Extreme reduction is also found in *Semiplotus*, but a characteristic surface and aortic channel morphology is apomorphic for this taxon.

It is thus concluded that particular details in the morphology of the basioccipital plate and posterior process can be useful indicators of relationship.

15. Posttemporal

Ctenopharyngodon (Fig. 12); broad, straight with long dorsal arm, basal part of the bone applied to the pterotic and intercalar, its upper part bridges the shallow posttemporal fossa to lie against the epioccipital. The anterior margin of the dorsal extension is bordered by a broad extrascapula.

Hypophthalmichthys (Fig. 12); elongate with a broad paddle-shaped basal portion, its upper half narrow and pointed distally. The anterior border of the bone curves round the posterior margin of the extrascapula. The *extrascapula* is elongate with an irregular anterior margin.

The *Ctenopharyngodon* type of posttemporal and extrascapula is widespread throughout the cyprinids and is regarded as plesiomorphic. The curved, spine-like posttemporal and narrow extrascapula of *Hypophthalmichthys* is otherwise present only in *Xenocypris*.

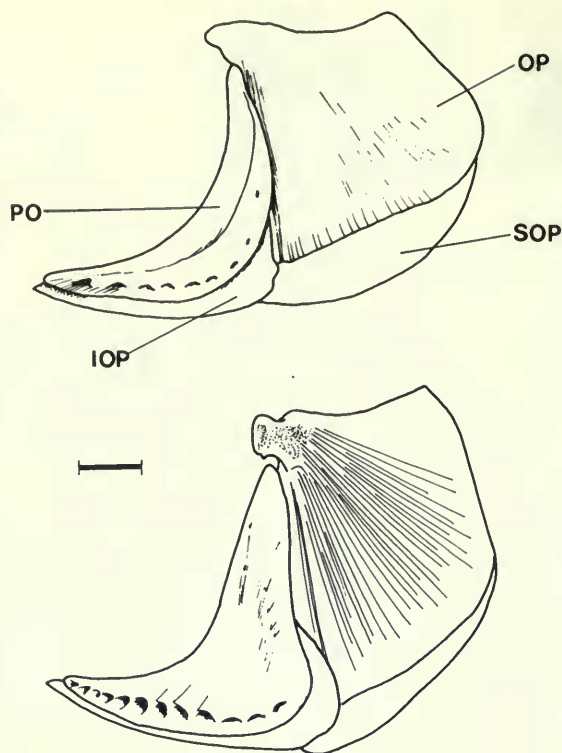


Fig. 20 Opercular bones: (upper) *Ctenopharyngodon idellus* BMNH 1861.1.17:6; (lower) *Hypophthalmichthys molitrix* BMNH 1895.5.31:22. Scale = 10 mm.

16. Opercular bones

Ctenopharyngodon (Fig. 20); preoperculum with a shallow horizontal limb containing 6 pores of the sensory canal system; operculum large, almost square.

Hypophthalmichthys (Fig. 20); preoperculum with deep horizontal limb containing 15 sensory pores; operculum large, deeper than long, its outer surface strongly ridged.

In both genera the basal part of the antero-dorsal opercular process (to which is attached the tendon of the *dilatator operculi* muscle) contains a tubular canal connecting the preopercular canal with the pterotic canal. The connection between the operculum and the pterotic in *Hypophthalmichthys* is effected through an ossified canal lying vertically above the opercular process. This small canal-carrying bone appears to be part of the dermopterotic.

There appears to be some variability in the morphology of the opercular sensory canal. Gosline (1974) noted that the preopercular canal ends 'blindly' or passes across the opercular face. However, where there is a connection between the preopercular and pterotic canals, it can be via a dermal opercular canal or 'suprapreopercula', an opercular tube or an epidermal connection. These varying conditions and their taxonomic significance are discussed in a separate paper (Banister & Howes, in preparation).

The opercular series, and particularly the size of the operculum are somewhat variable throughout the Cyprinidae but certain types of opercula can be associated with particular monophyletic groups. Examples are the bariliines where the opercular bones are almost always deep and narrow; the neobolines (*Chelaethiops*, *Neobolus*) where the opercula have an attenuated posterior margin; the chelines and aspinines where the opercula possess a long dorsal border. Caution must be exercised, however, in using opercula bone morphology as a phyletic character. Large opercular and expanded preopercular bones are to be found in such widely different trophic specialists as *Luciobrama*, *Barbus*, *Ctenopharyngodon* and

Hypophthalmichthys. In these taxa the similarity of opercular bone shapes appear to be the result of different functional demands which are at present not understood.

17. *Suspensorium*

Overall, there is a great similarity in the suspensorial elements of *Ctenopharyngodon* and *Hypophthalmichthys*.

The *palatine* is broad anteriorly in both genera. However, in *Ctenopharyngodon* articulation of the palatine head is with the lateral supraethmoid notch (see p. 5; Fig. 1). The more usual condition is for the palatine head to be at a lower level, almost in the plane of the preethmoid and to be attached by a ligament to either the anterior rim, the ventral surface of the supraethmoid, or to the upper part of the mesethmoid. Only in *Mylopharyngodon* and *Squaliobarbus* is the palatine head elevated as in *Ctenopharyngodon* and closely articulated with a lateral supraethmoid notch. The posterior part of the palatine in *Ctenopharyngodon* is rounded and articulates in a deep entopterygoid facet. The posterior region of the palatine in *Hypophthalmichthys* is laterally compressed and articulates with a shallow, narrow entopterygoid facet. Both types of posterior palatine articulation are encountered widely in cyprinids and it is not possible at present to say which is the more derived.

In both genera the *hyomandibula* is produced laterally and its articulatory dorsal border is steeply angled antero-ventrally. However, in *Ctenopharyngodon* there is a lateral shelf on the upper face of the hyomandibula and the ventral limb of the bone is short and broad, whereas in *Hypophthalmichthys* it is elongate. In both genera the *entopterygoid* and *metapterygoid* are depressed medially with the metapterygoid having a strongly concave dorsal border and a well-defined lateral ridge; the *quadrate* bears a wide ventro-lateral shelf, but in *Ctenopharyngodon* it is a larger bone than in *Hypophthalmichthys*.

There are differences in the form of the *symplectic* which is elongate in *Hypophthalmichthys* but short and deep in *Ctenopharyngodon*. This latter type appears to represent the more derived condition (see Howes, 1980), the elongate symplectic being common in Cyprinidae.

In general, there is uniformity of the suspensorial elements in the Cyprinidae; the variability is one of degree, usually involving elongations, deepening or medial depression of the bones.

18. *Jaws*

Ctenopharyngodon (Figs 21d, e, f); *maxilla* deep with a triangular midlateral ascending process; the anterior medial process is directed almost horizontally to contact its partner *via* a ligament; maxillary distal portion is broad, medially curved and produced into a ventral flange which contacts the distal part of the premaxilla. Approximately mid-way along the maxilla is a foramen sited below a lateral ridge (which serves as the attachment for the palatine ligament). The *premaxilla* is deep with only a short anterior ascending process its ventral edge is chisel-like. The *dentary* has a short, dorsally rounded coronoid process; the *anguloarticular*, a convex dorsal border.

Hypophthalmichthys (Figs 21a, b, c); *maxilla* shallow with a high, square midlateral ascending process; the anterior medial process is compressed and directed ventrad toward the midline; maxillary posterior portion is laterally compressed and ventrally extended to articulate with the premaxilla. The *premaxilla* is exceedingly shallow and thin with a short, broad, anterior ascending process and although its ventral edge is sharp, it is not bevelled as in *Ctenopharyngodon*. The *dentary* is shallow at the symphysis but deepens posteriorly and has a high, backwardly sloped coronoid process. The *anguloarticular* is short and deep with a long, steep dorsal border (60° slope to the horizontal).

The plesiomorphic cyprinid maxilla appears to be of the *Ctenopharyngodon* type, *viz* deep, with a large mid-lateral, or posteriorly placed ascending process with convex anterior, and concave posterior borders. Apomorphic derivatives involve the formation of a concave anterior border to the mid-lateral process as in *Hypophthalmichthys*, or complete reduction

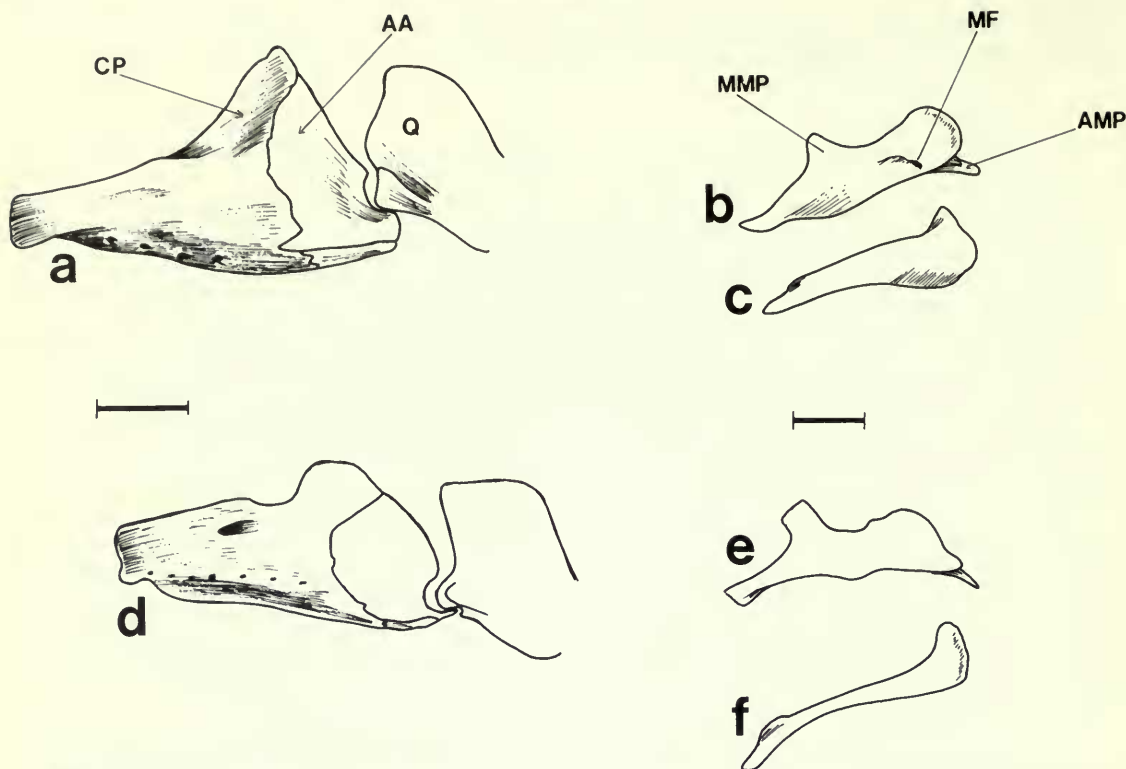


Fig. 21 Jaw bones in lateral view: *Hypophthalmichthys*, a. left dentary, b. right maxilla and c. right premaxilla; *Ctenopharyngodon*, d. left dentary, e. right maxilla and f. right premaxilla. Scales = 10 mm.

of the process as in some bariliines (see Howes, 1980). Another apomorphic feature of the maxilla appears to be the presence of an anterior foramen. This foramen provides the channel for a branch of the facial nerve which usually innervates an associated barbel. Although such a foramen is present in *Ctenopharyngodon*, there is no associated barbel and it will be argued later that this is due to secondary loss of the barbel (see p. 39). For the most part, however, it is true to say that those cyprinids with a maxillary foramen also have a rostral barbel. One cyprinid group which lack the maxillary foramen but have barbels are some bariliines (see Howes, 1980). However, in these taxa the barbel is not associated with the maxillary bone. The phylogenetic significance of these various conditions is discussed elsewhere (Banister & Howes, in preparation), but here it can be stated that the presence of a maxillary foramen is an apomorphic feature in one group of Cyprinidae (see also Banister & Bunni, 1980 : 157).

An L-shaped premaxilla without any dorsal or lateral protruberances is thought to represent the plesiomorph condition.

Although superficially alike, the lower jaws of *Ctenopharyngodon* and *Hypophthalmichthys* differ in the form of the coronoid process and anguloarticular. In the Cyprinidae the most common type of lower jaw morphology is one where the coronoid process occupies a central position and is formed entirely from the dentary. In these cases the anguloarticular has an almost horizontal dorsal border (eg. *Barbus*, *Leuciscus*, *Aspius*, *Culter*; see fig. 36 in Howes, 1978). Contribution of the anguloarticular to the coronoid may be considered derived and associated with orientation of the jaw and a shift in mandibular muscle insertions. A lower jaw element which may be worthy of more critical attention in cyprinids is the *coronomeckelian* bone. It commonly occurs as a deep, short bone with a well-developed shelf along its medial face to which attaches the tendon of part of the *adductor*

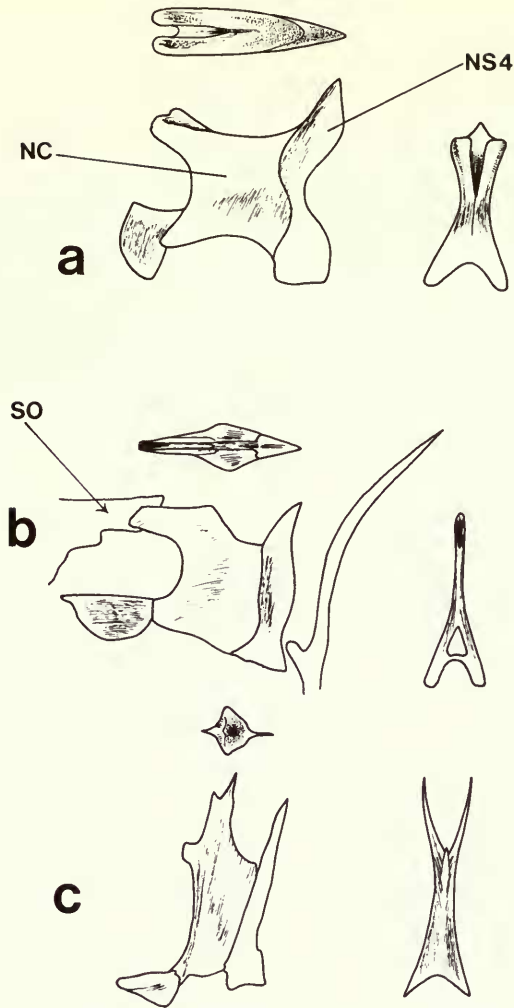


Fig. 22 Anterior dorsal vertebral elements shown in lateral, dorsal and anterior views of: a. *Ctenopharyngodon*; b. *Hypophthalmichthys*; c. *Abramis brama*. Semi-diagrammatic, compiled from several specimens; all drawn to same scale.

mandibulae complex. There is some variation in the shape of this bone and certainly in one group of 'leuciscines' its spear-shaped appearance seems to offer an apomorphic character of phyletic value (Howes, in preparation). The morphology of the lower jaw is possibly the most variable anatomical unit in Cyprinidae, relative growth of its various parts probably being a major contributing factor to this variability.

19. Vertebral column

Ctenopharyngodon (Fig. 22a); 1st vertebra compressed and with laterally directed processes, 2nd with an elongate lateral process, 4th with anteriorly sloping pleural rib and backwardly sloping neural spine. Weberian complex: tripus broad, sickle-shaped; ossa suspensoria making extensive medial contact and forming a posteriorly curved transverse septum. Total number of vertebrae 43 (4 + 22 + 16 + 1).

Hypophthalmichthys (Fig. 22b); 1st vertebra with caudally directed lateral processes, 2nd with short, triangular, caudally directed processes, 4th with anteriorly sloping pleural rib and upright neural spine. Weberian complex: tripus elongate with mesially curved tip, ossa

suspensoria extensive forming an antero-ventrally sloping transverse septum, neural complex bifurcated and articulating with supraoccipital. Total number of vertebrae 39–40 (4 + 18–19 + 16 + 1).

The most striking differences in the morphology of the vertebral column in *Ctenopharyngodon* and *Hypophthalmichthys* occur in the anterior vertebrae forming the Weberian complex. The neural complex of *Ctenopharyngodon* is antero-dorsally expanded and curved forward so that its anterior tip is above the 1st vertebra (Fig. 22a); there is no contact with the supraoccipital. In *Hypophthalmichthys* the neural plate is deep and lamellate with a concave anterior border. The antero-dorsal prong is bifurcated and the supraoccipital process contained within the fork (Fig. 22b). The dorsal margin of the neural plate is deeply grooved for the midline ligament, as it is in the aspinines (see Howes, 1978 : 19).

In the Cyprinidae contact between the supraoccipital crest and the neural complex is uncommon. It occurs in *Labeo*, *Catla*, *Osteobrama* and *Semiplotus*, but in these taxa there is no deeply grooved dorsal margin to the neural complex, and the anterior bifurcation is either shallow or lacking. Only in *Xenocypris* does the neural complex have nearly the same morphology as in *Hypophthalmichthys*. However, a well-developed lamellate neural plate is commonly encountered in the Cyprinidae and may be a plesiomorphic character. In *Abramis*, *Rutilus* and some species of *Chondrostoma* the neural complex has no antero-dorsal extension but is perpendicular or anteriorly inclined and deeply forked; a condition unique in cyprinids (Fig. 22c). In some catostomids (*Carpoides*) there is contact between the supraoccipital and neural complex. Here the condition is similar to that in *Labeo* where the neural plate is lamellate and without a dorsal groove or anterior bifurcation.

It seems likely that in the latter cases expansion of the neural complex (? fused 3rd and 4th supraneurals) and its contact with the supraoccipital is associated with a deepened body and the forceful forward probing movements of the head when feeding. Reinforcement of the anterior part of the vertebral column and rigidity of the posterior cranium is provided by this arrangement. In *Hypophthalmichthys* which is essentially a mid-water or surface feeder, this feature must serve a different purpose and may be associated with some elevation of the cranium during feeding.

The common (plesiomorph) condition of the first four (Weberian) vertebrae in Cyprinidae is as in *Ctenopharyngodon* (the typical condition is seen in *Opsaridium microcephalus*, Howes, 1980, fig. 39D). Similar development of the transverse processes, tripus and ossa suspensoria similar to those of *Hypophthalmichthys* is encountered elsewhere in members of the 'Leuciscinae' (ie *Leuciscus*, *Abramis*) and the aspinine group. However, elongation of these elements is also found in some barbines, chelines and neobolines (eg. *Chelaethiops*) and its usefulness as an indicator of phyletic relationship is doubtful.

20. Gill-arches

Ctenopharyngodon has no particular modifications of the gill arches, which are similar to those of other cyprinids. The gill-rakers are short and spiny, biserially arranged and almost horizontally placed on the arch so that they intermesh with those on the neighbouring arch to form a filter.

Hypophthalmichthys displays marked modification of the gill arches and possesses a complex epibranchial organ (Figs 24–26).

The gill structures of *Hypophthalmichthys* have been described in varying detail by a number of authors. Boulenger (1901) first described the epibranchial organ; Fang (1928) gave a detailed description of the gill arches and epibranchial organ, and speculated on their function. Zambriborshch (1955; 1957) described and figured the gross morphology of the branchial apparatus and histology of the gill-rakers, including comments on function. Verigin (1957) described and figured the epibranchial organ, gill-rakers, upper pharyngeal pad and roof of the pharynx. He also studied the ontogeny of the branchial apparatus. Wilamowski (1972) made a description of the epibranchial organ and gill-rakers, comparing them with the branchial system of *Cyprinus*. Taken *in toto* these descriptions give an

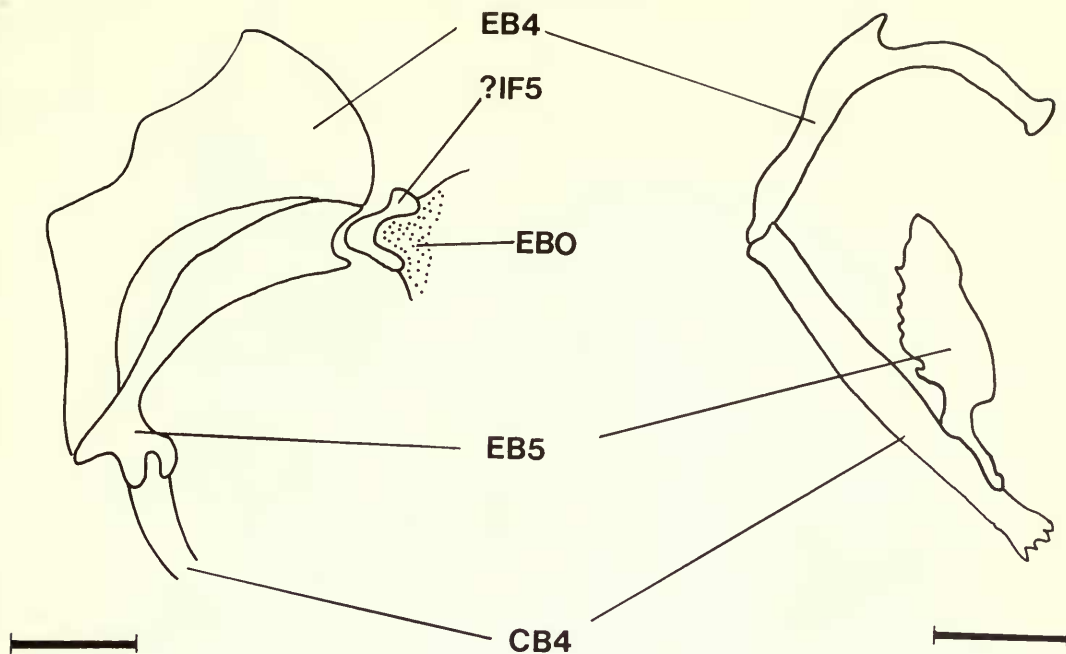


Fig. 23 Posterior gill-arch elements: (left) *Hypophthalmichthys molitrix*, from dissected specimen BMNH 1895.5.31 : 22; (right) *Xenocypris argenteus* from alizarin specimen BMNH 1889.6.8 : 19. Left scale = 5 mm, right = 2 mm.

adequate account of the organ's morphology, and it is necessary here only to emphasize certain of its apomorph characters.

The *ceratobranchials* are elongate, bearing numerous biserially arranged slender gill-rakers. The two rows of rakers are set at a diverging angle to one another thus producing an 'interbranchial space' (Fang, 1928). There are approximately 13–14 rakers per 1 mm of ceratobranchial. Fang (1928) recognized two types of gill-rakers, broad and narrow, the broad type occurring between each 4th and 5th narrow type. The gill-rakers are connected by a reticulate mucuous membrane (sifting membrane of Fang, 1928) which forms a network or filter, whose pores are about 20μ in diameter. The gill-rakers continue onto the epibranchials.

The 1st and 4th *epibranchials* are expanded dorsally into axe-shaped elements. The 1st forms the anterodorsal wall, and the 4th the posteromedial wall of the epibranchial organ (the branchial arches are so orientated that the 4th epibranchial comes to lie in a medial (longitudinal) plane rather than a posterior (transverse) one). Although not entirely ossified, a 5th epibranchial is present as a well-developed, broad, lamellate element, and has a complex articulation with the 4th ceratobranchial (Fig. 23).

There are two large well-ossified *infrapharyngobranchials* recognized as IF2 and IF3; IF4 is represented by an extensive cartilaginous bloc bordering the posterior rim of IF3 and contacting epibranchials 3 and 4 (Fig. 24). In front of IF2 there is another large cartilaginous cap onto which articulates epibranchial 1. This no doubt is IF1. In adult specimens the 5th epibranchial is joined to the capsule of the epibranchial organ *via* an interposed cartilage which may represent the 5th *infrapharyngobranchial*.

The *epibranchial organ* is formed by four curled cartilaginous channels or ducts, which are prolongations of the four epibranchials (Fig. 26). Each duct is lined with two rows of biserially arranged gill-rakers, the posterior row of one arch intermeshing with the anterior row of the adjacent arch and in this way running into each duct (Fig. 24). The outer row of the 1st arch enters a small chamber of the first duct and becomes reduced in size and number. The first duct houses the gill-raker rows of the 1st and 2nd epibranchials, the 2nd those of the

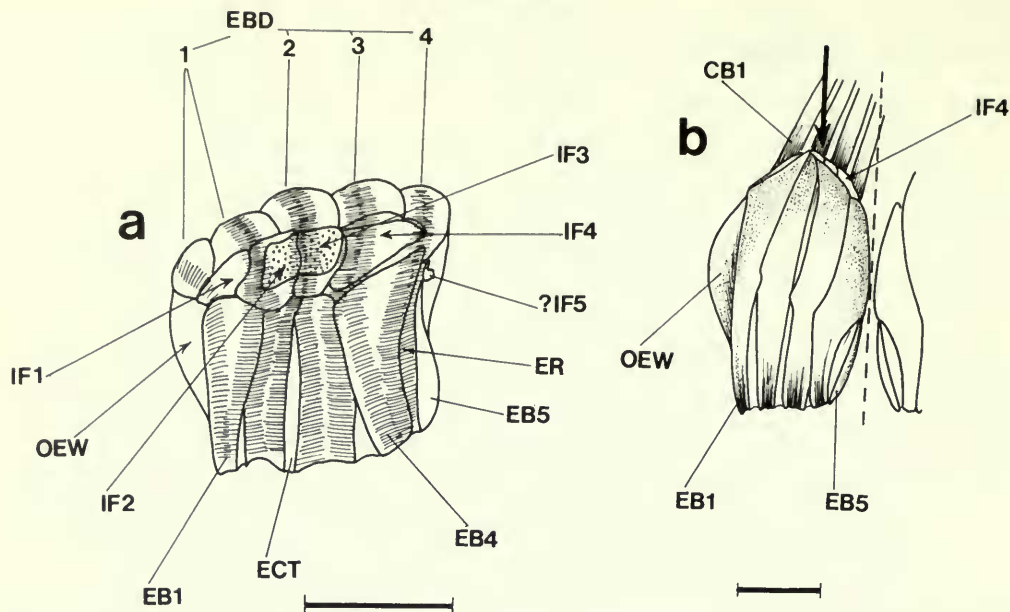


Fig. 24 *Hypophthalmichthys* epibranchial organ: a. anterior view of left organ, ossified areas of the infrapharyngobranchials are stippled; b. dorsal view of left organ to show orientation, dashed line represents the ventral midline of the head, and solid arrow indicates the direction of view depicted in a. Scales = 10 mm.

2nd and 3rd epibranchials, the 3rd those of the 3rd and 4th, and the 4th duct those of the 4th and 5th epibranchials. Zambriborshch (1957) referred to the organ ducts as supra- and infrapharyngobranchials. However, the infrapharyngobranchials are here identified as elements distinct from the cartilaginous ducts.

The entire epibranchial structure is invested in palatal connective tissue. The tissue below the basal part of the organ is produced into four folds (palatal folds of Fang, 1928) which hang down into the interbranchial channels (Figs 25 & 26). The lateral face of the epibranchial organ, also formed from palatal tissue, is connected to the medial face of the preoperculum via a segment of the *adductor hyomandibulae* muscle (= *pharyngopraepercularis* muscle of Zambriborshch, 1955); see Fig. 25.

The morphology of the epibranchial arches in *Hypophthalmichthys* is unique. Modified gill-arches and gill-rakers are, however, found elsewhere in cyprinids. In *Xenocypris argenteus* the epibranchials are rounded over a thickened palatal tissue pad, the gill-rakers are numerous, approximately 25 per 1 mm of gill-arch, and extend to the proximal part of the epibranchial. The infrapharyngobranchials extend into the dorsal surface of the palatal tissue pad. The pads or cushions have a hollow interior, the internal surface of the tissue is highly papillose and convoluted. Similar development of the epibranchials, gill-rakers and palatal cushions are to be found in *Plagiognathops*, although the gill-rakers on the 1st arch are 'normal' and the palatal cushion is more papillose.

An hypothesized plesiomorph condition of the epibranchial organ is encountered in *Abramis*. Here the epibranchials are markedly rounded and the palatal tissue greatly thickened. This is particularly evident in *Abramis sapa* where the palatal cushion occupies a large part of the pharyngeal cavity (Fig. 27b). Anteriorly it is rounded and forms a cup-shaped depression in the palate. The palatal cushion resembles that of *Xenocypris* in having a hollow interior, although not as cavernous. The outer surface of the cushion shows slight ridging between the gill-arches, reminiscent of the palatal folds in *Hypophthalmichthys*. The cartilaginous proximal tips of the epibranchials are highly developed and lie embedded in a cartilaginous casing which extends along the basioccipital (Figs 27a, b). Again, as in

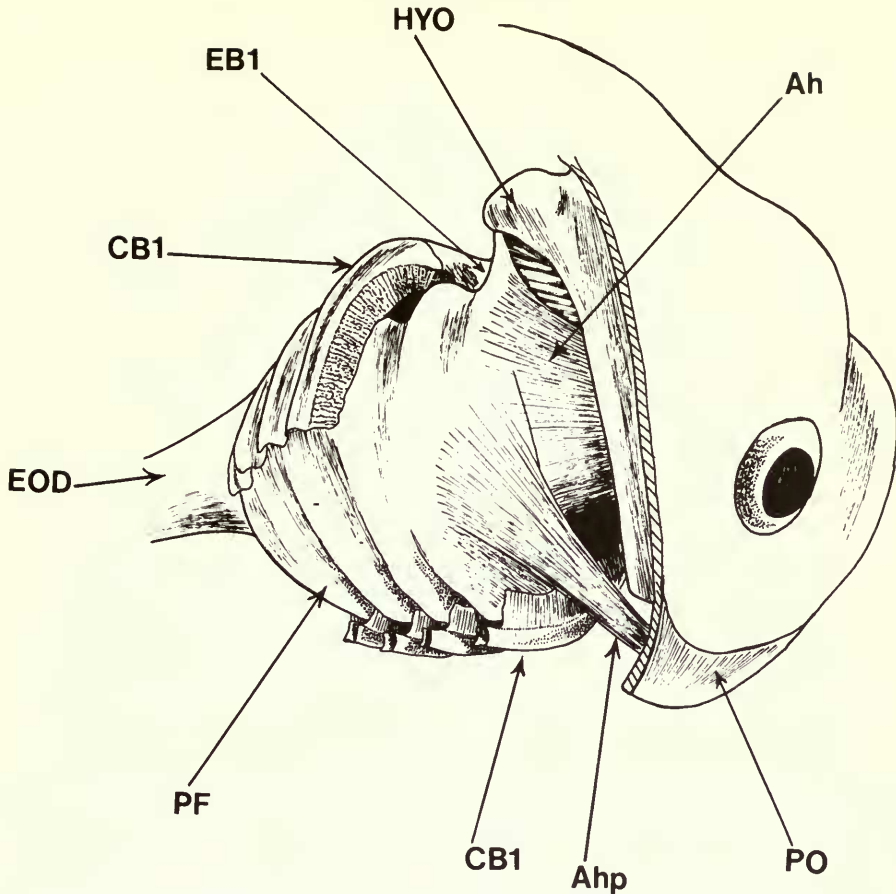


Fig. 25 *Hypophthalmichthys*, postero-lateral view of epibranchial organ and gill-arch elements. The ceratobranchials have been partly cut away to show the organ's folded tissue surface. Schematic drawing based on two dissected specimens.

Xenocypris the cartilaginous tips of the epibranchials extend ventrally into the floor of the palatal cushion roof.

Elsewhere in the Cyprinoidei an epibranchial organ is present in Catostomidae. In these taxa as in *Hypophthalmichthys* and the xenocyprinids, the epibranchials are rounded over a complex pharyngeal pad and are medially prolonged (Fig. 28a). In catostomids the pharyngeal pad more closely resembles that in *Xenocypris* being a medially undivided structure surrounding the basioccipital process, and not in the form of paired diverticula as in *Hypophthalmichthys*. The catostomid basioccipital is expanded laterally and is fretted, playing an integral part in the structure of the pharyngeal cushion. This is unlike the cyprinid condition where the basioccipital acts as a support for connective tissue dividing the organ (see Weisel, 1960 for an account of the catostomid pharyngeal organ, and Eastman, 1977 for a description of catostomid pharyngeal anatomy).

When compared to the epibranchial organs of other teleosts which possess them, that of *Hypophthalmichthys* most closely resembles the continuous tube organs of some clupeids (see Miller, 1969).

It is possible that a form of epibranchial organ occurs in the south-east Asian cyprinid genus *Thynnichthys*. This fish shows a remarkable superficial resemblance to *Hypophthalmichthys*, particularly in its low positioned eye. As in the latter, the gill-arches are elongate but they lack gill-rakers. There does, however, appear to be a swollen area of pharyngeal

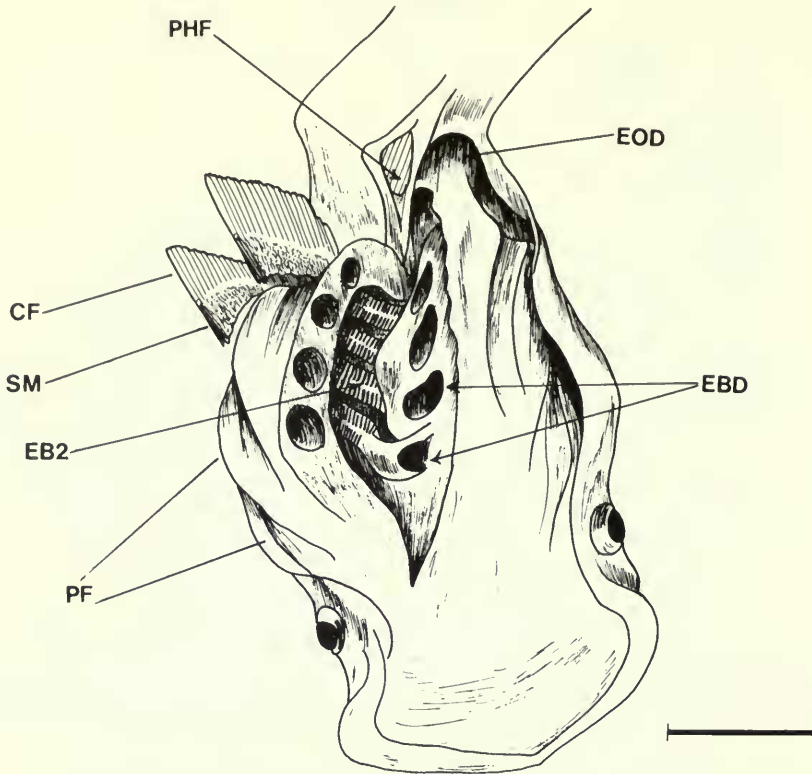


Fig. 26 *Hypophthalmichthys*, ventral dissection of the epibranchial organ, ceratobranchials cut away. Scale = 10 mm. Drawn from specimens BMNH 1895.5.31 : 36-37 and uncatalogued Swinhoe specimen.

tissue with a single posterior median duct leading into the oesophagus. Only a single specimen is available for superficial dissection but those osteological features which are observable are unlike those of *Hypophthalmichthys* and more closely resemble *Amblypharyngodon*.

Although Berry & Low (1970) described certain morphological features in hybrids between *Hypophthalmichthys* and *Ctenopharyngodon*, no mention was made of the development of an epibranchial organ.

A specialization of the upper branchial arch shared by *Hypophthalmichthys* and *Xenocypris* is hypertrophy of the 5th epibranchial. In *Xenocypris* this element is broadly lamellate and has a form of articulation with the 4th ceratobranchial similar to that of *Hypophthalmichthys* (Fig. 28a). In cyprinids the 5th epibranchial is greatly reduced or appears as a small cartilaginous element above the 4th epibranchial (Banister, pers. comm.). The hypertrophy of this element and its articulation with the 4th epibranchial are seen as synapomorphies uniting *Hypophthalmichthys* and *Xenocypris*.

A superficially similar gill-arch morphology to that in *Hypophthalmichthys* occurs in *Gibelion* and *Catlacarpio* (Fig. 28d). In these taxa also the ceratobranchials are elongate and bear numerous gill-rakers. The epibranchials are sickle-shaped, their medial 'handle' portion being dorso-ventrally expanded and antero-posteriorly compressed. The two infra-pharyngobranchials are thickened, IF2 being virtually reorientated from the usual horizontal plane to a vertical one. The entire upper branchial basket is surrounded by a thick, papillose pharyngeal cushion and this, together with the fretted basioccipital pharyngeal process greatly resembles the upper pharyngeal anatomy of catostomids. It may be that the catline taxa employ similar feeding methods to those of catostomids (see Weisel, 1960). Again, similarly developed epibranchials are present in '*Labeo*' *stoliczkae* (Fig. 28c), but they are

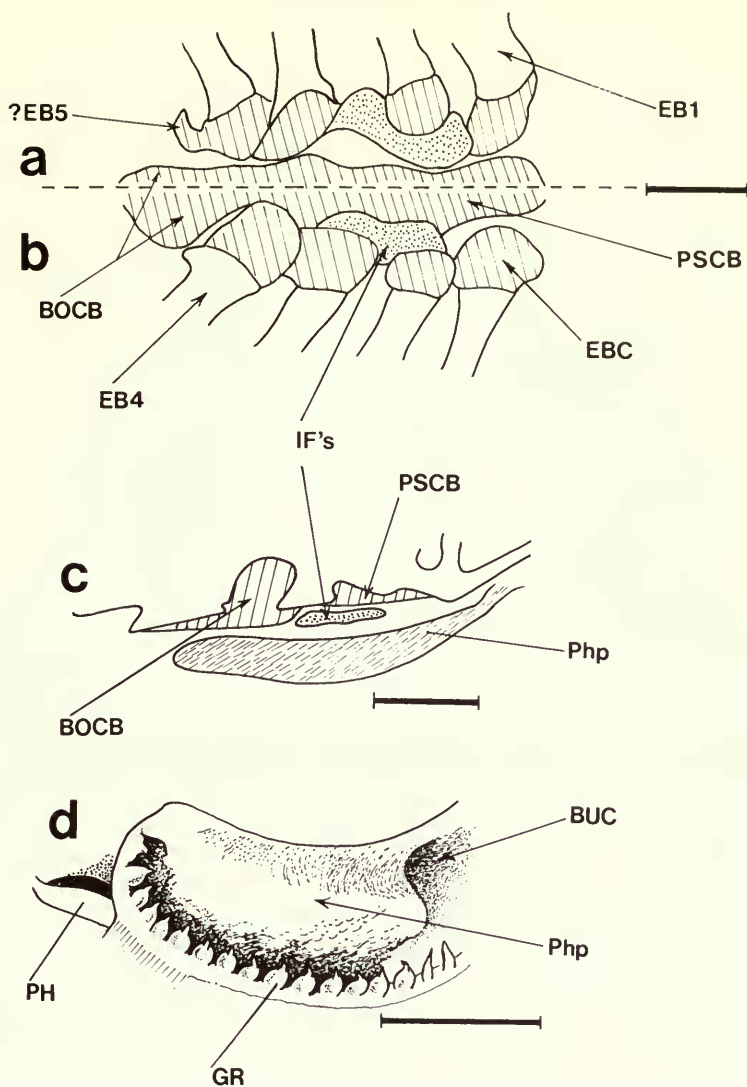


Fig. 27 Upper pharyngeal anatomy of *Abramis*. Dorsal branchial elements of: a. *Abramis brama*, left side BMNH 1974.9.5 : 1-31; b. *Abramis sapa*, right side BMNH 1967.7.17 : 3-4, drawn *in situ*, scale = 1 mm; c. lateral view of cartilaginous basicranial bloc and pharyngeal pad in *A. brama*, scale = 10 mm; d. pharyngeal cavity of *A. sapa* showing 4th ceratobranchial from which most of the gill filaments have been removed, scale = 5 mm.

not so acutely curved medially, and neither are the infrapharyngobranchials orientated in the same way. Furthermore, the basioccipital process is thick and broad. Other neurocranial characters suggest that '*Labeo*' *stoliczkae* has as its closest relative, *Cirrhina*, whilst *Gibelion* and *Catlacarpio* seem closely related to *Thynnichthys*, *Amblypharyngodon* and *Osteobrama* (part).

Pharyngeal bones and teeth of both genera have been described and figured by Chu (1935). The pharyngeal bone of *Ctenopharyngodon* has a greatly attenuated lower limb and there is a prominent process (for the attachment of the posterior portion of the *levator posterior*) at the curvature of the upper limb. The teeth are in two rows (2, 4-5), greatly compressed and with their grinding surfaces serrate, the serrations being the lateral margins of grooves on the tooth's outer face.

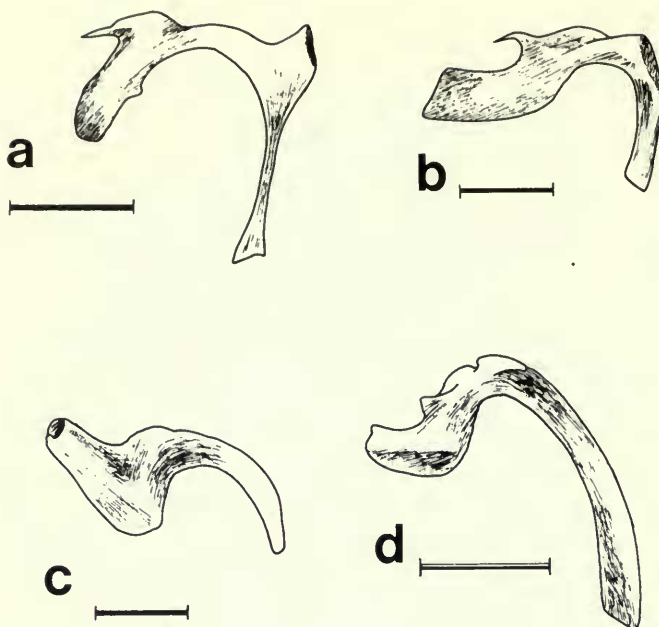


Fig. 28 Posterior views of the right 4th epibranchial of: a. *Xenocypris argenteus* BMNH 1889.6.8 : 19-22 (alizarin); b. *Abramis ballerus* (uncatalogued skeleton); c. *Labeo stoliczkae* BMNH 1891.11.30 : 286 (skeleton); and d. *Gibelion catla* BMNH 1908.12.28 : 1122 (skeleton). Scales for a, b, and c = 2 mm, d = 5 mm.

According to Chu (1935), the teeth and pharyngeal bone of the *Hypophthalmichthinae* '... are singularly unique, without parallel in other cyprinids'. The anterior limb of the pharyngeal bone is dorsoventrally depressed and the upright posterior limb is antero-posteriorly compressed. There is a large fenestra within the expanded dentigerous part of the bone. *In situ* this fenestra is covered laterally by a translucent tissue, medially it serves as a cavity into which the expanded edge of the basioccipital masticatory plate inserts (Fig. 26). The 4 teeth of *Hypophthalmichthys* are in a single row, are compressed, have a concave occlusal surface with a transverse median groove and lateral striation.

Chu (1935) is correct in describing the pharyngeal dentition of *Hypophthalmichthys* as unique. There are, however, similarities between the pharyngeals of this species and those of *Xenocypris* and *Plagiognathops*, where there is also an extensive foramen in the pharyngeal bone, and the teeth have similar grinding surfaces (see Chu, 1935).

21. Adductor hyomandibulae muscle

In *Ctenopharyngodon* the adductor hyomandibulae is developed as in the majority of cyprinids, namely, a thick dorsal element arising from the face of the prootic and inserting, muscously, on the upper medial face of the hyomandibula.

In *Hypophthalmichthys* the muscle is expanded and is continuous (see below) with the adductor arcus palatini, forming a muscular 'wall' which effectively separates the branchial and buccal cavities. The upper part of the muscle (Dahm, Fig. 29) arises from the prootic and inserts on the upper medial face of the hyomandibula as in other cyprinids. However, a posterior segment attaches to the antero-dorsal wall of the epibranchial organ and another part of the (? same segment) of muscle runs from the lateral wall of the epibranchial organ to the preoperculum (*pharyngopraeopercularis* of Zamborshch, 1955). Anterior to the dorsal part of the muscle another element can be distinguished originating from the lower part of the prootic and the pterosphenoid spur to insert on the medial section of the hyomandibula. Anteriorly this second portion is continuous with the adductor arcus palatini

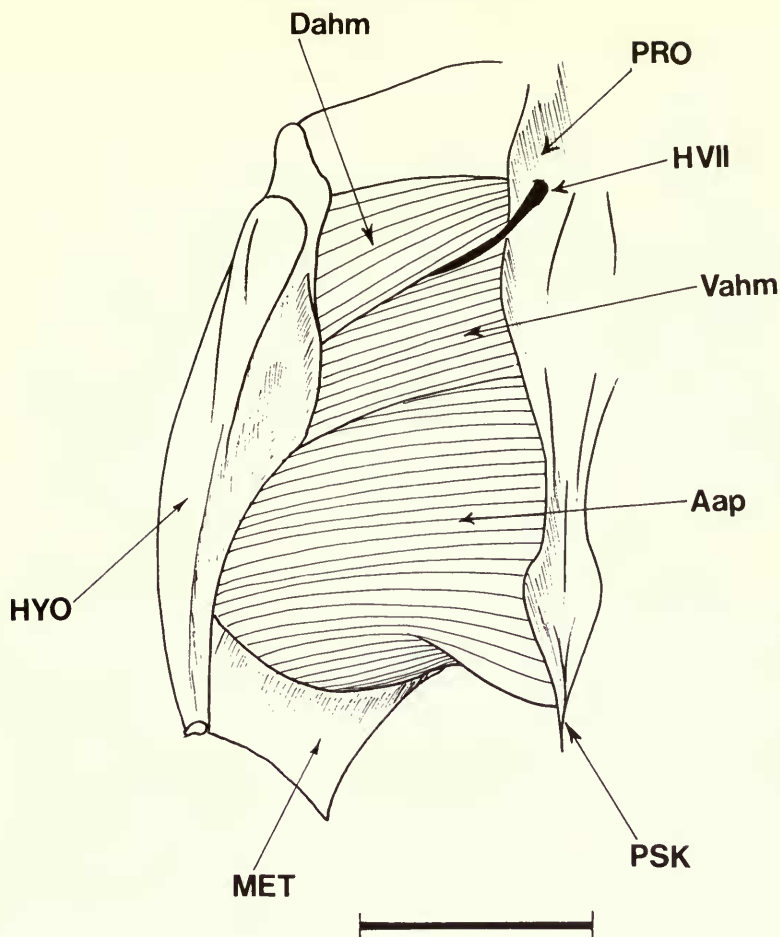


Fig. 29 *Hypophthalmichthys*, ventro-posterior view of adductor hyomandibularis musculature, based on specimens BMNH 1895.5.31 : 36-37. Scale = 10 mm.

muscle which originates from the parasphenoid ventral process and inserts along the lower limb of the hyomandibula and, anteriorly, along the dorsal rim of the metapterygoid. Winterbottom (1973) points out that the *adductor hyomandibulae* and, at least in certain taxa, the *adductor arcus palatini* are parts of a single muscle. Certainly, in this case it is only the orientation of the fibres that distinguishes the upper medial section of the muscle as part of the *adductor hyomandibulae* rather than as part of the *adductor arcus palatini*.

Such a highly developed *adductor hyomandibularis* musculature occurs elsewhere only in *Abramis*, *Rutilus* and *Chondrostoma*. In *Abramis* the upper medial portion of the muscle is strongly attached to the pharyngeal tissue, and thence to the posterior border of the hyomandibula. Although in *Xenocypris* the *adductor hyomandibulae* is not as expansive as in the other genera, the upper medial section is attached, along its entire ventral surface, to the tissue covering the branchial arches, and some fibres appear to extend on to the preoperculum. Morphologically, this can be considered a forerunner of the derived condition realized in *Hypophthalmichthys* where part of the *adductor hyomandibulae* becomes attached to the epibranchial organ and preoperculum and possibly acts as the power unit forcing water through the epibranchial ducts. The *adductor hyomandibulae* morphology in *Hypophthalmichthys*, *Xenocypris*, *Abramis*, *Rutilus* and *Chondrostoma* is considered synapomorphic.

22. Pectoral girdle

The pectoral girdle of *Ctenopharyngodon* is remarkably similar to that of *Barbus* and *Cyprinus*, except that the posterior cleithral lamina is extended posteriorly. The horizontal cleithral limb is broad, with a concave anterior border. The cleithra contact each other only at their anterior tips. The coracoid is shallow and rounded posteriorly; the mesocoracoid is narrow.

The pectoral girdle of *Hypophthalmichthys* displays many modifications relative to the presumed plesiomorph pattern. The horizontal cleithral lamina is greatly expanded and rises in the vertical plane to join its partner for the anterior third of its length. The posterior border of the coracoid is square. The mesocoracoid limb is broad. In both genera the postcleithra are elongate and curved mesially, ie. plesiomorphic state; see Howes (1980).

In no other cyprinid is the horizontal cleithral lamina expanded to the same extent as in *Hypophthalmichthys*. Only in *Abramis* and *Xenocypris* is there an approachable condition. In these taxa, however, the medial cleithral border is deeply notched at a point just below the dorsal articulation of the mesocoracoid. The function of this notch is to contain the expanded border of the pharyngeal bone. The mesocoracoid limb is broad in all these taxa.

Phylogenetic relationships

From the foregoing descriptions and analyses of *Ctenopharyngodon* and *Hypophthalmichthys*, a series of apomorph characters can be identified, none of which is shared by both taxa. Instead, these characters serve to relate the respective genera to other taxa and thus *Ctenopharyngodon* and *Hypophthalmichthys* must be considered members of two distinct monophyletic assemblages.

Relationships of *Ctenopharyngodon*

The following characters are identified as apomorphies.

1. Subtemporal fossa extending anteriorly to invade the autosphenotic on which part of the pharyngeal musculature originates (p. 15)
2. Lateral notch in the supraethmoid with which the palatine head articulates (p. 5)
3. Extensive prootic with ventrally directed trigemino-facialis foramen (p. 13)
4. Extensive intercalar forming posterior corner of cranium and contributing to an accessory subtemporal fossa (p. 22)
5. Divided *levator posterior* muscle, the posterior segment originating from the intercalar (p. 22)
6. Extensive and bullate epioccipital (p. 21)
7. Reduced lateral occipital fenestra (p. 21)
8. Olfactory foramen countersunk entirely within the lateral ethmoid (p. 9)
9. Frontal broad and sloping ventrally (p. 18)
10. Massive and shelved supraorbital (p. 20)
11. Orbital portion of parasphenoid broadened and with ventral ridge (p. 11)
12. Ventrally directed pterosphenoïd process (p. 10)
13. Thickened 1st infraorbital (p. 20)
14. Distally broadened and upwardly curved basioccipital pharyngeal process (p. 23)

Characters 1–6 are synapomorphies with *Mylopharyngodon* and *Squaliobarbus*; 7–11 with *Mylopharyngodon*; 12–14 are autapomorphic.

From the distribution of these apomorph characters, *Mylopharyngodon* is considered to be the sister taxon of *Ctenopharyngodon* with both forming the derived sister group of *Squaliobarbus*. These three taxa constitute a monophyletic lineage termed the *Squaliobarbine* group.

Mylopharyngodon (Fig. 30b) is a monotypic genus (type species *M. piceus* (Richardson, 1845)), characterized by the autapomorphic features of an extensive bowl-like masticatory

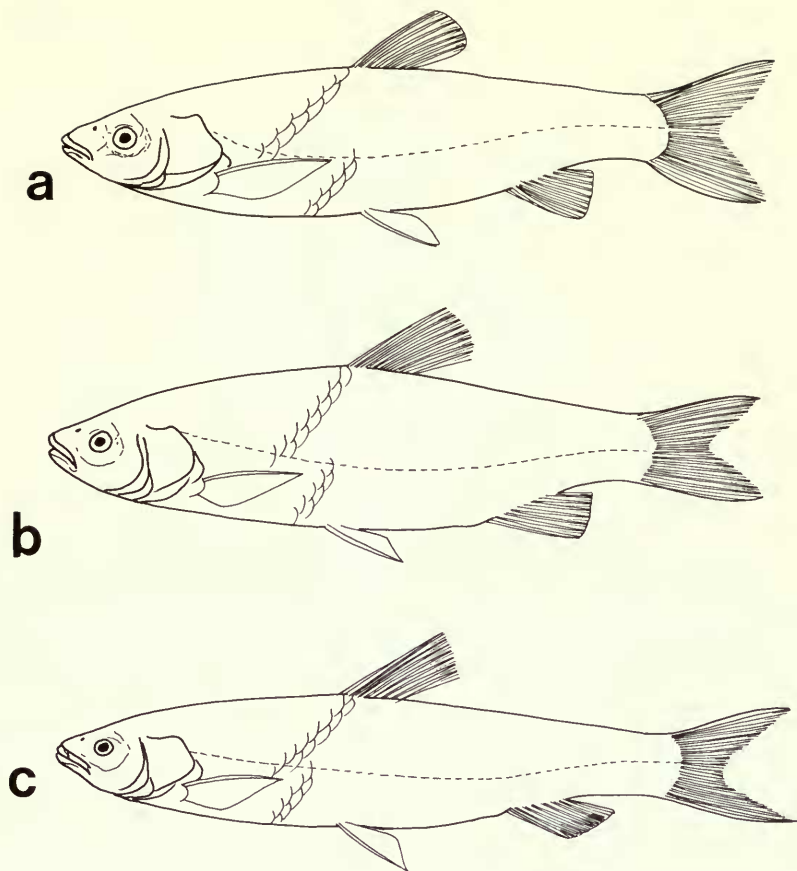


Fig. 30 Outline drawings of members of the *squaliobarbine* group: a. *Ctenopharyngodon idellus*; b. *Mylopharyngodon piceus*; and c. *Squaliobarbus curriculus*.

plate (Fig. 19b); large molariform pharyngeal teeth; small basioccipital facet dorsally overlapped by an exoccipital ridge (Fig. 31); and narrow, mesially curved posterior cleithral lamina.

Squaliobarbus (Fig. 30c) is the plesiomorph member of the lineage differing from its sister taxa in possessing two pairs of small barbels. The anterior pair of barbels are minute and appear superficially as mere appendages of the ventral infraorbital skin fold. However, the barbel is innervated by a sub-branch of the VII facial nerve. The main nerve branch passes through a foramen in the maxilla just below a shelf which forms the attachment point of the palatine ligament. The barbel originates some distance posterior to the maxillary foramen and the main nerve branch supplies the lip fold.

It was stated on p. 28 that a maxillary foramen carrying a nerve supply to an anterior barbel is an apomorph character uniting those taxa which possess it. It was also noted (p. 28) that *Ctenopharyngodon* has a maxillary foramen but both nerve and barbel are lacking. In *Mylopharyngodon* there is no trace of a maxillary foramen or barbels.

Two hypotheses are proposed to account for the distribution of barbels and associated foramina amongst squaliobarbines:

1. That *Ctenopharyngodon* and *Mylopharyngodon* represent a plesiomorph condition in which the foramen and/or barbel has not formed.
2. That the absence of barbels and associated nerve in these genera represents secondary losses.

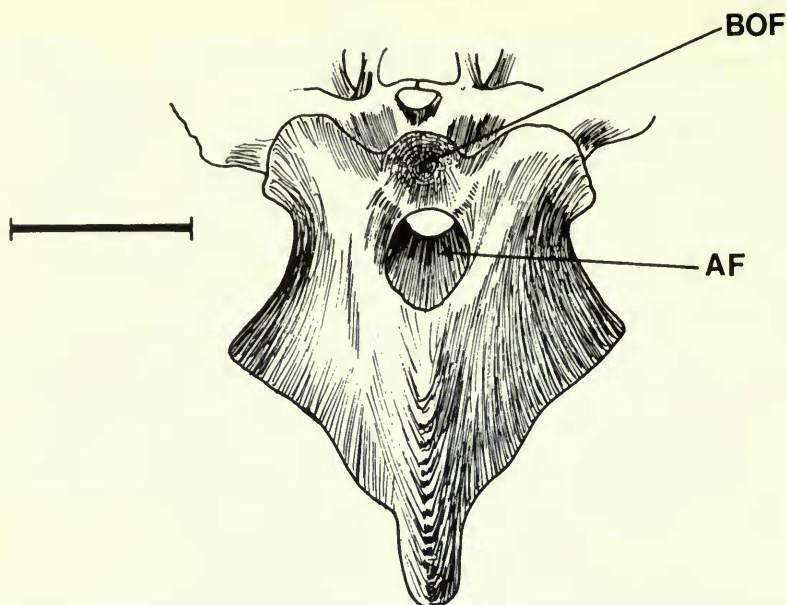


Fig. 31 *Mylopharyngodon piceus*; posterior view of basioccipital from specimen BMNH 1895.5.31 : 40. Scale = 5 mm.

It is assumed that the second hypothesis is more likely to be the correct one as the plesiomorph lineage (*Squaliobarbus*) possesses barbels, and that in this taxon their reduction and that of the associated nerve signifies transition to loss state. Also, reduction of barbels is recorded in other cyprinid taxa (see Banister & Bunni, 1980).

The distribution of cyprinid barbels; anterior and posterior, whether they are associated with a foramen, the type of nerve supply and form of proximal attachment is a subject dealt with elsewhere (Banister & Howes, in preparation). For the purposes of this discussion it is considered that the squaliobarbine assemblage form part of that series of taxa which possess a maxillary foramen carrying a nerve supply to an anterior barbel.

The suite of apomorph characters defining the squaliobarbines involves, for the most part, the occipital region of the cranium—the expansion of the subtemporal fossa and the intercalar. These osteological features are concomitant with an increased evolutionary development of the *levator posterior* muscle which extended forward into the autosphenotic and was divided posteriorly, the posterior section originating from the intercalar. These specializations could be associated with the essentially phytophagous habits of the squaliobarbine taxa.

The proposed theory of relationships is to regard the squaliobarbine group as a divergently specialized sister lineage to all other barbelled Cyprinidae (i.e. Cyprininae); see Fig. 32.

Synopsis of taxa assigned to the Squaliobarbine group

Ctenopharyngodon Steindachner, 1866

Pristiodon Dybowski, 1877

Type and only species: *C. idella* (Valenciennes, 1844).

Distribution: Pacific drainage of the USSR and China, lat. 50°–23°N.

Introduced into many tropical and temperate areas including Europe, North America, India, New Zealand, Malaysia.

Principal bibliographic sources concerning biology: Lin, 1935; Nikolsky, 1954; Inaba & Nomura, 1956; Hickling, 1967; Okada, 1960; Cross, 1969; Edwards, 1974.

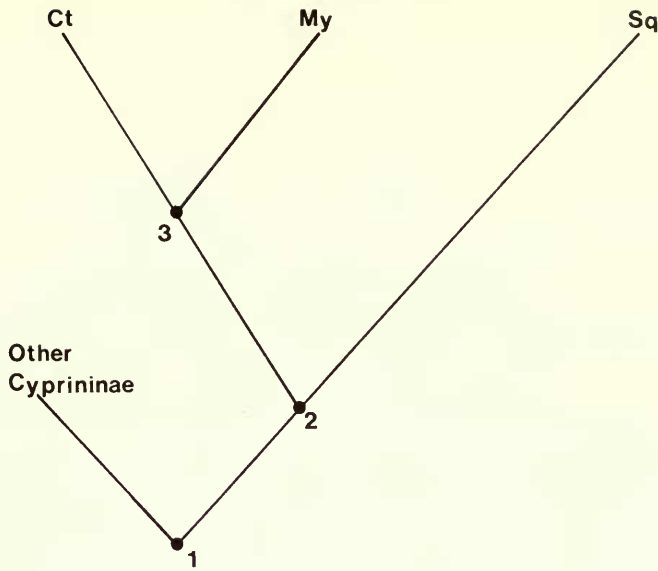


Fig. 32 Cladogram representing the phyletic relationships of the *squaliobarbine* group. Ct = *Ctenopharyngodon*, My = *Mylopharyngodon*, Sq = *Squaliobarbus*. Node 1. Possession of maxillary foramen. Node 2. Synapomorphies 1–7 (page 38). Node 3. Synapomorphies 8–11 (page 38), also loss of maxillary foramen in *Mylopharyngodon*.

***Mylopharyngodon* Peters, 1873**

Myloleucus Günther, 1873

Myloleuciscus Garman, 1912

Leucisculus Oshima, 1920

Type and only species: *M. piceus* (Richardson, 1845).

Distribution: Amur, China, Formosa.

Principal bibliographic sources: Nikolsky, 1954 & 1956.

***Squaliobarbus* Günther, 1868**

Type species: *S. curriculus* (Richardson, 1845).

Sauvage (1884) described another species, *S. caudalis*, from Tonkin. Pellegrin (1934), when commenting on the Hanoi collection of Sauvage, made no mention of this species but included in his list, *S. curriculus*.

Distribution: Amur, China, Western Korea, Hanoi.

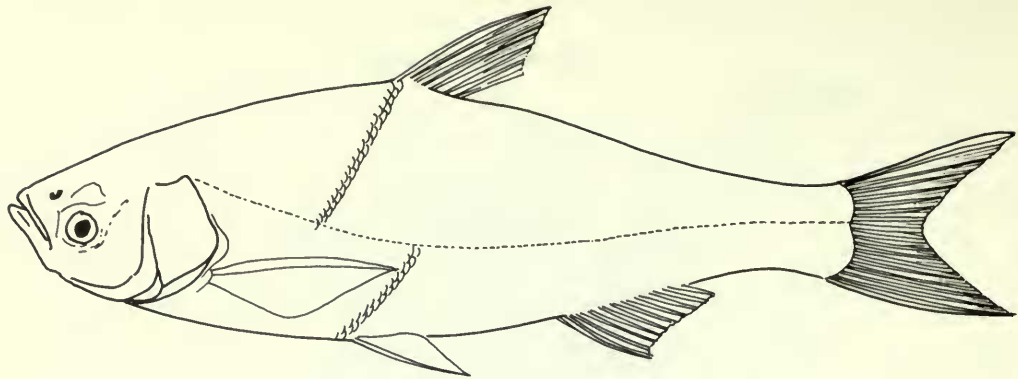
Principal bibliographic source: Nikolsky, 1956.

Relationships of *Hypophthalmichthys*

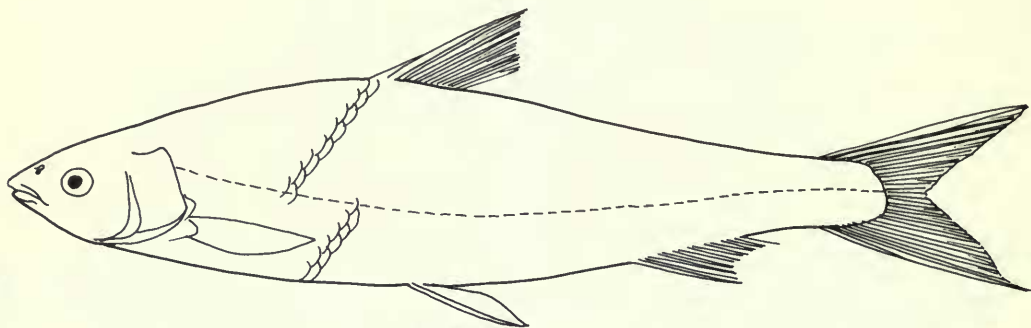
The following characters are identified as apomorphies:

1. Medial ethmoid notch floored by the vomer (p. 9)
2. Frontal with an acute lateral slope, providing an extensive cranial dilatator fossa (p. 15)
3. Extensive lateral occipital fenestra (p. 21)
4. Modification of the *adductor hyomandibulae* muscle involving partial attachment to the preoperculum and upper pharyngeal tissue (p. 36)
5. Expanded horizontal cleithral lamina (p. 38)
6. Markedly rounded epibranchials (p. 33)
7. Deep basioccipital keel with marked concave anterior border (p. 23)
8. Carotid foramen contained in ventrally produced parasphenoid process (p. 12)
9. Lateral ethmoid-frontal fenestra (p. 9)
10. Expanded 1st and 4th epibranchials, the 5th present and hypertrophied (p. 34)

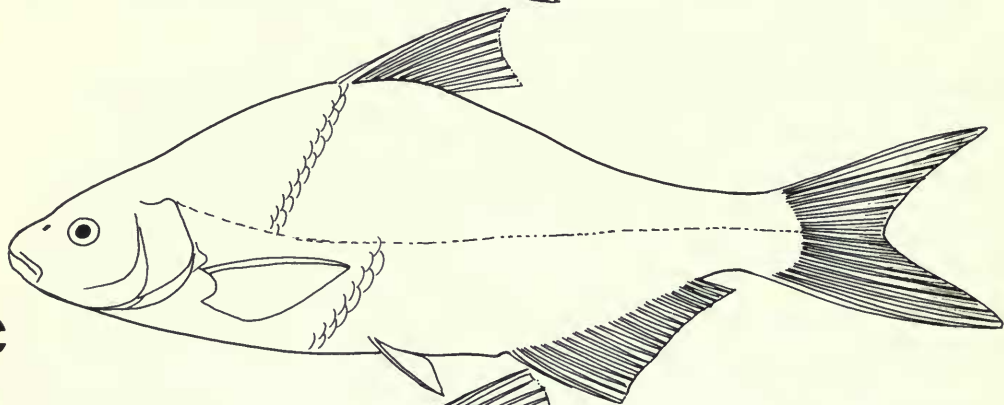
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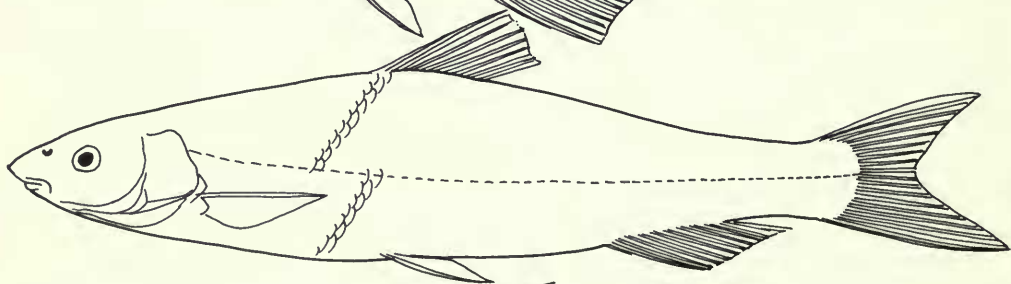
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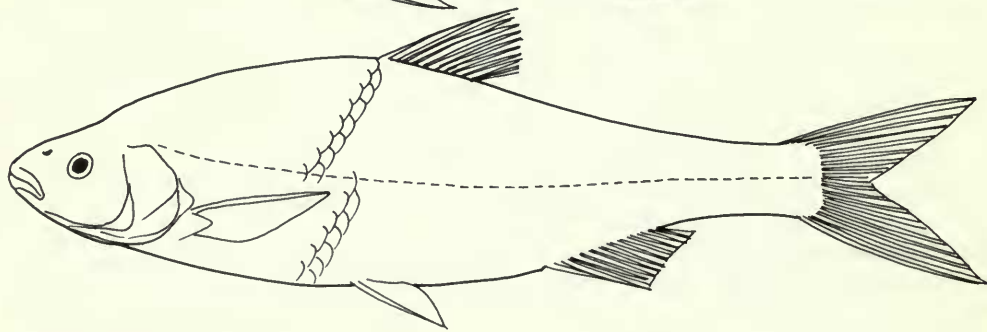
c



d



e



11. Extensive fossa in pharyngeal bone (p. 36)
12. Exoccipital wing extended distally to contact pterotic spine (p. 21)
13. Curved posttemporal (p. 25)
14. Pterosphonoid contributing to anterior trigemino-facialis foramen (p. 10)
15. Cardiform masticatory plate with tubular posterior extension (p. 23)
16. Intercalar invading border of exoccipital (p. 22)
17. Complexly developed epibranchial organ (p. 31)
18. Neural complex bifurcated and articulating with supraoccipital (p. 30)

Characters 1–6 are synapomorphic with *Abramis* and *Xenocypris* (?*Plagiognathops* and *Distoechodon*); 7–13 with *Xenocypris*; 14–18 are autapomorphic.

From the distribution of these apomorph characters *Xenocypris* is regarded as the twin taxon to *Hypophthalmichthys*. Together they form the sister group to an assemblage including *Abramis*.

Xenocypris (Fig. 33b). The taxonomy of this genus is confused, two other monotypic taxa, *Plagiognathops* and *Distoechodon* being regarded by some authors as subgenera (see Bănărescu, 1970). All these taxa are presently placed in the subfamily Xenocyprinidinae.

Two previous comments regarding *Xenocypris* are in need of modification. The first (Howes, 1979), was to the effect that the Xenocyprinidinae was polyphyletic, viz that the included genera, *Xenocypris*, *Plagiognathops* and *Distoechodon* shared no derived characters. In fact they do (see below). The second statement (Howes, 1980) was that the closest relatives of *Xenocypris* are amongst the hemicultrines (*Hemiculter*, *Hemiculterella* and *Ochetobius*). This assumption was based on what are now deemed to be symplesiomorphies, and indeed, the hemicultrines as earlier conceived represent a paraphyletic assemblage.

Plagiognathops and *Distoechodon* share with *Xenocypris* (as represented by the type species *X. argenteus*) apomorph characters involving the gill-arches and basioccipital, although they are not so highly derived as in *Xenocypris*. Lack of osteological material prevents a complex diagnosis of the character complexes and the three genera are considered together as an unresolved trichotomy.

Abramis (Fig. 33c), here including the 'genera' *Vimba* and *Blicca*; see p. 46, shares with *Xenocypris* and *Hypophthalmichthys* synapomorphic characters 1–6, involving the ethmoid region, cranial roof, pharyngeal roof covering and associated musculature. However, a simple sister-group relationship between *Abramis* and *Xenocypris* + *Hypophthalmichthys* is doubtful in the light of other apomorphies possessed by *Abramis* and exclusively shared with *Chondrostoma* and *Rutilus* (Figs 33d & e). These are:

- (i) confluent ventral channelling of the parasphenoid and basioccipital;
- (ii) columnar, dorsally bifurcated neural complex; and
- (iii) gill-rakers with globular, papillate bases.

The underlying synapomorphy (Saether, 1979) uniting *Rutilus*, *Chondrostoma*, *Abramis*, the *Xenocypris* complex and *Hypophthalmichthys* is a modification of the basicranium, viz a parasphenoid notch or confluent ventral channelling of the parasphenoid and basioccipital, and deepening of the basioccipital process. From the distribution of synapomorphies within this assemblage—termed the *Abramine group*—two hypotheses of generic relationships are available and represented as cladograms A & B (Fig. 34).

In cladogram A, *Abramis* is reckoned to be the sister group of *Rutilus* and *Chondrostoma* (the similarity between the parasphenoid-basioccipital morphology links these two genera as sister taxa) on the basis of characters (i) and (ii) cited above. In this case, the characters *Abramis* shares with *Hypophthalmichthys* and the *Xenocypris* complex (listed as synapomorphies 1–6 on p. 41) must be considered as convergent.

In cladogram B, *Abramis* is considered as the sister group to *Hypophthalmichthys* + the

Fig. 33 Outline drawings of members of the *abramine group*: a. *Hypophthalmichthys molitrix*; b. *Xenocypris argenteus*; c. *Abramis brama*; d. *Chondrostoma nasus*; e. *Rutilus rutilus*.

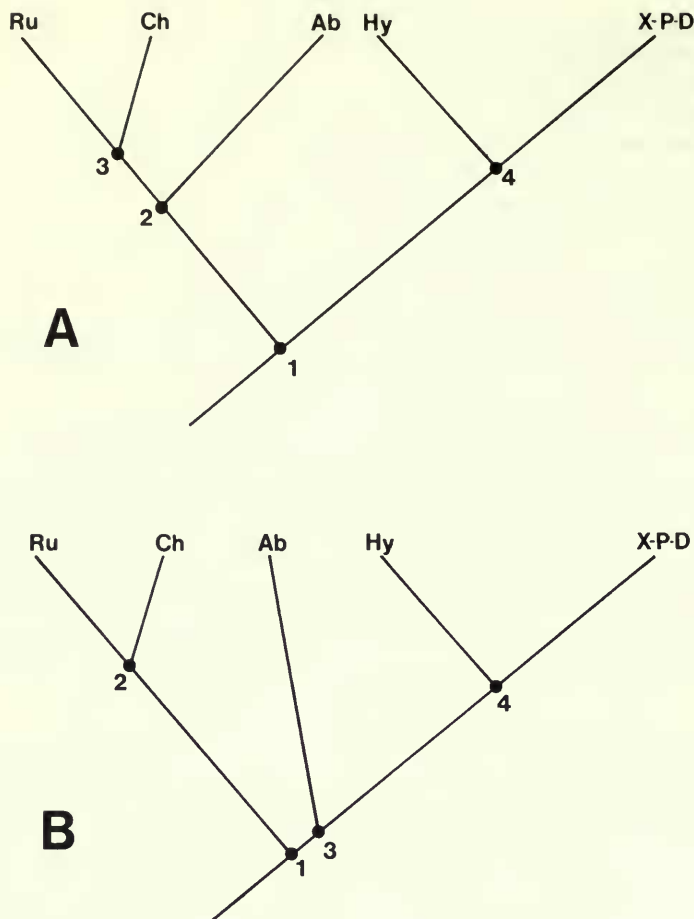


Fig. 34 Cladograms expressing two schemes of phyletic relationships of the *abramine* group. Ru = *Rutilus*, Ch = *Chondrostoma*, Ab = *Abramis*, Hy = *Hypophthalmichthys*, X-P-D = *Xenocypris-Plagiognathops-Distoechodon* trichotomy.

Cladogram A. Node 1. Modification of basioccipital-parasphenoid; development of pharyngeal pad; transversely convex vomer; hypertrophy of *adductor hyomandibulae* muscles. Node 2. Basioccipital-parasphenoid channel; columnar neural complex; globular based gill-rakers. (Convergence of 6 characters in *Abramis* with *Hypophthalmichthys* and *Xenocypris*.) Node 3. Synapomorphic basioccipital morphology (see Fig. 18). Node 4. Synapomorphic gill-arch structure; development of epibranchial organ and associated basicranial deepening. (Loss of convex vomer and deep ethmoid in *Hypophthalmichthys*.)

Cladogram B. Node 1. Combination of nodes 1 and 2 in cladogram A. Node 2.= node 3 in cladogram A. Node 3. Synapomorphies 1–6 (p. 41). Node 4. Synapomorphies 7–13 (p. 41); also loss of 5 characters through nodes 1–3 (see text, p. 43).

Xenocypris complex. In this case, five characters must be recognized as having been secondarily lost in the two latter taxa, viz: parasphenoid-basioccipital channel; columnar neural complex; globular based gill-rakers (lost in both *Hypophthalmichthys* and *Xenocypris*); convex and deeply notched ethmoid (lost in *Hypophthalmichthys*).

It may be argued that in their vertebral elements *Hypophthalmichthys* and *Xenocypris* are conservative and have retained the plesiomorphic lamellate neural complex. Likewise, *Hypophthalmichthys* may have retained the plesiomorphic ethmo-vomerine bloc. (No evidence is available to show that apomorphic modifications of the ethmoid region are linked with those of the basicranium.) If this is so, then the more likely hypothesis is that

Rutilus, *Chondrostoma* and *Abramis* form the sister group to *Hypophthalmichthys* and the *Xenocypris* complex, as one has only to postulate the loss of the apomorphic ethmo-vomerine assembly in *Hypophthalmichthys* (cladogram A). This is also the more likely hypothesis of relationships if the autapomorphic parasphenoid-basioccipital and neural complex of *Abramis* are seen as terminal points of a possible evolutionary sequence represented by the more plesiomorphic types in *Rutilus* and *Chondrostoma*.

Although it may appear that *Abramis* displays an incipient form of the epibranchial structure in *Xenocypris*, this is misleading. In fact, the gill-arch morphology and pharyngeal dentition suggests that the pharyngeal pad of *Abramis* differs functionally from that of *Xenocypris* and its relatives. There is indeed, no 'morphocline' or 'transitional' series represented in extant abramine genera which might reflect the evolutionary development of an epibranchial organ. However, the basic architectural modification of the basicranium (deepening of the parasphenoid and basioccipital) can be seen as a preadaptation to the formation of an epibranchial structure which in the abramines appears to have followed two evolutionary pathways hypothesized to be most closely represented by the relationships expressed in cladogram A. Falsification of either hypothesis will be forthcoming when more complete anatomical data are available for *Plagiognathops* and *Distoechodon* and a functional analysis of pharyngeal/epibranchial mechanisms available for all abramine taxa.

Synopsis of taxa assigned to the Abramine group

***Hypophthalmichthys* Bleeker, 1860**

Cephalus Basilewsky, 1855

Abramocephalus Steindachner, 1869

Onychodon Dybowski, 1872

Aristichthys Oshima, 1915

Type species: *H. molitrix* (Valenciennes, 1844).

Two other species, *H. nobilis* (Richardson, 1844) and *H. harmandi* Sauvage, 1884 are included. Reasons have already been given for synonymizing *Aristichthys* (p. 2)

Distribution: Amur, China. Introduced into Taiwan, Thailand, Japan, Sri-Lanka, Europe and North America.

Principal bibliographic sources concerning biology: Tsui, 1936; Nikolsky, 1956.

***Xenocypris* Günther, 1868**

Type species: *X. argentea* Günther, 1868.

Another 9 or 10 species are recognized by various authors; see Bănărescu (1970) for most recent revision, and Nikolsky (1956) for biological data.

***Plagiognathops* Berg, 1907**

Type and only species: *P. microlepis* (Bleeker, 1871).

Distribution: Yangtze, middle Amur, Ussuri, Lake Khanka (see Berg, 1949).

***Distoechodon* Peters, 1880**

Type and only species: *D. tumirostris* Peters, 1880.

Distribution: Southern China.

***Rutilus* Rafinesque, 1820**

Scardinius Bonaparte, 1837

Hegerius Bonaparte, 1845

Acanthobrama Heckel, 1843

Leucos Heckel, 1843

Pigus Bonaparte, 1845

Cenisophius Bonaparte, 1845

Gardanus Bonaparte, 1845

Pararutilus Bonaparte, 1845

Pachychilon Steindachner, 1866

Rubellus Fitzinger, 1873

Mirogrex Goren, Fishelson & Trewavas, 1973

Type species: *R. rutilus* Rafinesque, 1820.

Numerous nominal species with a wide distribution throughout Europe, USSR, Israel to the Tigris and Euphrates.

The characters used to define Leuciscine genera are criticized below (p. 48). Typical are the use of modal numbers of fin rays, lateral line scales, gill-rakers and plesiomorphically low vertebral counts. No comparisons of the osteology of the various 'genera' given in the above synonymy have been made previously. I have compared the osteology of *Rutilus rutilus* with a selection of species currently assigned to this genus, to *Scardinius*, to *Acanthobrama* and to *Mirogrex* and am unable to find any noticeable differences. Indeed, all these taxa possess those apomorph characters which identify *Rutilus*, viz form of the median ethmoid notch; extension of the vomerine arms; preethmoid not, or barely contacting the mesethmoid; columnar neural complex; globular, papillate based gill-rakers.

Scardinius is usually separated from *Rutilus* on the basis of its having the pharyngeal teeth in two rows instead of a single row, and the presence of a ventral body keel. I would consider that the differences in pharyngeal teeth are of a specific nature, as in *Abramis* (see Shutov, 1967 and Eastman & Underhill, 1973); likewise, the ventral keel is variously developed in *Rutilus rutilus*. Wheeler (1976) concluded that of the features used to characterize *Rutilus* and *Scardinius* the morphology of the pharyngeal teeth was probably the most significant. If Chu's (1935) hypothesis is accepted, namely that three rows of pharyngeal teeth represent the primitive (plesiomorph) condition, then the two rows of *Rutilus* and the single row of *Scardinius* are seen as successively derived states. In the majority of *Rutilus* × '*Scardinius*' hybrids a second tooth row is apparent which may indicate a dominant genetical pattern for the plesiomorph condition.

Concerning the synonymy of *Acanthobrama* and *Mirogrex*; Goren, Fishelson & Trewavas (1973) separate these two genera on modal differences in the number of lateral line scales, gill-raker counts and the number of vertebrae. These authors compare the two 'genera' with *Capoetobrama* (see below), but not with *Rutilus*, and they state that the generic position of the presumed ancestral taxon to *Acanthobrama*, '*Rutilus*' *tricolor* '... has not been determined'. I would agree that the species *tricolor* does not belong to *Rutilus* and should properly be placed amongst a complex including *Leucaspis*. However, *Acanthobrama* and *Mirogrex* share all the apomorph characters of *Rutilus sensu stricto*, they are thus to be regarded as belonging to that genus. The genus *Capoetobrama* (see above) does not belong to this assemblage at all and may be more closely allied to the alburnine group (unpublished obs.).

Abramis Cuvier, 1817

Ballerus Heckel, 1843

Blicca Heckel, 1843

Zopa Fitzinger, 1873

Vimba Fitzinger, 1879

Leucabramis Smitt, 1895

Sapa Kazanskii, 1928

Type species: *A. brama* (Linnaeus, 1758).

Five or six species with wide distribution in Europe, the Baltic, Black, Aral and Caspian seas; Asia Minor, Caucasus.

Principal bibliographic source: Backiel & Zawisza, 1968.

Shutov (1969) considered *Blicca* synonymous with *Abramis*. His analysis of populations of *Blicca bjoerkna* revealed a morphometric range encompassing that of *Abramis brama* and a decrease in the numbers of teeth in, and ultimate loss of the second tooth row across the range of the samples. Similarly, I find no differences in the osteology of *Abramis* and *Vimba*.

Both genera possess an identical form of parasphenoid-basioccipital border with ventral channel and notch and highly developed pharyngeal tissue pads. They also share the apomorphic feature of a scaleless pre-dorsal fin ridge. Characters formerly used to separate these 'genera', such as the position of the anal fin origin and the presence of a dorsal ridge on the caudal peduncle are continuously variable and meaningless as taxon defining criteria. All *Abramis* species display considerable morphometric variability (see Berg, 1949 and Bănărescu, 1963).

***Chondrostoma* Agassiz, 1835**

Type species *C. nasus* Agassiz, 1835.

Berg (1949) records 18 species, having a wide distribution throughout Europe south to the Tigris and Euphrates.

Chondrostoma is characterized by those autapomorphic characters associated with forshortening and deepening of the upper jaw bones and a forwardly inclined coronoid process on the dentary. The posterior extension of the pharyngeal plate is thin and broad with a grooved dorsal surface. Assertions made concerning *Chondrostoma* in the anatomical descriptions presented here refer only to the type species, *C. nasus*.

Discussion

Earlier comments (Howes, 1976) that few, if any, presently recognized cyprinid subfamilies are monophyletic (in the sense of Hennig, 1966) have been amply reinforced by this study. Two genera, *Ctenopharyngodon* and *Hypophthalmichthys* previously included in the Leuciscinae are here identified as representative of two monophyletic lineages only distantly related.

As noted above (p. 28), the presence of a maxillary foramen (or its suggested past presence) associated with a rostral barbel is considered apomorphic for one branch of a diphyletic division of the Cyprinidae. It is to this assemblage that the monophyletic lineage (squaliobarbine group) containing *Ctenopharyngodon* belongs. *Hypophthalmichthys* is contained within the abramine group and belongs to that assemblage of taxa lacking the maxillary foramen. It is the majority of these taxa which are provisionally recognized as the subfamily Leuciscinae.

Nikolsky (1954) made a similar dichotomous classification of the Cyprinidae. In one branch he included leuciscines, *Aspius* '... and other fish', the other he represented by *Barbus*, *Cyprinus* and *Gobio*. Nikolsky did not give formal recognition to these divisions and retained the formerly recognized subfamilies without assigning them to one or other lineage.

The following discussion is concerned mainly with the classification and intrarelationships of the non-barbelled cyprinids (Leuciscinae).

Classification of the Leuciscinae

The 'subfamily' Leuciscinae (originally a division introduced by Bonaparte, 1846) has long been used as a category for containing 'generalized' cyprinids, including approximately 40% of Old-World genera. Not all authors have accepted the Leuciscinae; Berg (1949) assigned the majority of Old-World genera to the Cyprininae. On the other hand, Hubbs & Lagler (1958) extended the geographical range of the Leuciscinae to embrace New-World genera. Gosline's (1978) concept of the Leuciscinae embraced also the Cultrinae. These decisions demonstrate a lack of methodology in determining cyprinid supraspecific relationships.

As it stands, the Leuciscinae includes at least four monophyletic assemblages; aspinine (Howes, 1978), abramine (reported herein), alburnine and phoxinine (unpublished) all of which are interrelated to other non-barbelled cyprinids presently recognized as four monophyletic lineages; bariliine (Howes, 1980), cheline (Howes, 1979), hemicultrine (Howes, 1978, part) and cultrine (Howes, 1978, part). It seems, however, that none of these groups is a likely candidate for the status of sister-group to the abramines.

Identification of the abramine sister-group is hampered by the non-resolution of the monophyly of the nucleus of the Leuciscinae, the genus *Leuciscus*. It appears that part of *Leuciscus* is related to the aspinine group and another possibly forms the sister-group to the abramines. Characters supporting an abramine-*Leuciscus* relationship are the presence in some species of *Leuciscus* of an incipient ventral basioccipital channel and a similarity in the ethmovomerine region.

Abramis has been thought by some authors to be related to the American cyprinid genus *Notemigonus* (Miller, 1958 : 203; Bănărescu, 1973). Contrary to this idea I find no synapomorphies linking *Notemigonus* to any member of the abramine group. At this point it must be stated that New-World Cyprinidae have not been surveyed in depth in an attempt to formulate their relationships with any element of the Old-World Leuciscinae. Only *Ptychocheilus* has been examined in detail and would seem (together possibly with *Algansea*) to share apomorphies with the Old-World aspinine group (work in preparation). Whilst it may well be that New-World genera such as *Notropis* and *Chrosomus* are closely related to the Eurasian *Phoxinus* (see Mahy, 1975), it is quite wrong to consider them as synonymous (Bănărescu, 1973). It must be borne in mind that *Phoxinus* as it stands is also a paraphyletic group and such is likely to be the status of *Chrosomus* and *Notropis*.

Christopher & Linder (1979) note the close similarity between *Chondrostoma* and the American *Acrocheilus*. Certainly the jaw morphology of both taxa are alike but no other cranial features demonstrate a close relationship.

At some level, of course, the New-World cyprinids must form sister groups of the Old-World. Whether they represent a single monophyletic sister group to one or other of the monophyletic lineages contained within the 'Leuciscinae' or comprise several lineages forming twin taxa with other non-barbelled Old-World groups (cultrines, chelines, etc) are theories which remain to be tested.

Leuciscine hybrids

Futuyama (1979) notes that '... typological thinking focuses first on the "pure" forms and then interprets intermediate phenotypes as secondary products. If we focused on the continuum of phenotypes as a unit, we might not worry as much about which are the species and which the hybrids'.

Futuyama's statement is supported by a revised concept of leuciscine genera. Former hypotheses for the relationships between leuciscine genera have depended upon degree of genetic compatibility as demonstrated by hybridization. The measure of relationship being determined by terminal development stage of offspring, survival rate and reproductive viability. A contrary opinion regarding the validity of hybridization in a phylogenetic context has been expressed by Rosen (1979). Rosen regards reproductive compatibility as a plesiomorphy marked by mosaic distribution within a group. This hypothesis would certainly account for those conflicting cases amongst cyprinids where supposedly phylogenetically closely related taxa fail and distantly related ones succeed in being reproductively compatible. Such inconsistencies are usually explained away as misidentification of parental stocks. Suzuki's (1968) explanation for one such conflicting result was that '... Some Soviet species of Leuciscinae are probably more closely related to Cyprininae than Japanese species of Leuciscinae'. Such a statement disregards any kind of rigorous methodology in elucidating phylogenetic relationships.

A greater number of *naturally occurring intergeneric hybrids* have been reported for Leuciscine genera than for possibly any other group of teleosts (see Schwartz, 1972). A more rigorous (cladistic) definition of these genera reduces many cases of *intergeneric to interspecific* hybridization (ie. crosses between '*Vimba*' '*Blicca*' × *Abramis* (Berg, 1949), '*Aristichthys*' × *Hypophthalmichthys* (Voropayev, 1969), '*Scardinius*' × *Rutilus* (many reports, see Schwartz, 1972). Naturally occurring intergeneric hybrids are judged to be so on the basis of intermediacy of characters, notably the pharyngeal dentition. A typical example of the use of 'intermediate' characters is given by Berg (1949 : 88–89) for a 'hybrid' popula-

tion of *Leuciscus cephalus* × *Chalcaburnus chalcoides*. As enumerated, these characters could well describe a populational variant of one of the presumed parental species.

A similar argument can be applied to many so-called *interspecific hybrids*. The likelihood is that they are not crosses but clinal or other populational fragments. The numerous subspecies and varieties described in Leuciscine genera by Berg (1949) indicate a considerable degree of populational variability. This of course is not to deny that interspecific hybridization does occur.

Wheeler (1976) notes that high levels of hybridization amongst cyprinid taxa occur in areas where recent introductions have been made. Certainly, nearly all the records I have checked for 'intergeneric' European cyprinid hybrids have been cases involving one or both of the taxa being recently introduced into a 'new' ecological situation.

I conclude that 'hybridization' amongst cyprinid taxa must be treated with caution and is a useless character as a measure of phylogenetic affinity.

Classification of the 'true' carps

The squaliobarbine group belongs to the great assemblage of taxa characterized by the presence of a maxillary foramen and (usually) an associated rostral barbel (see p. 28). As yet no accounts of monophyletic groups, other than the squaliobarbines (dealt with herein), have been published, although Reid (1978, unpublished thesis) has identified a labeoine group. The hypothesis proposed above (p. 40) that the squaliobarbines form the sister group to all other barbelled carps is a temporary expedient. But, with available data I am unable to offer a more worthwhile solution. Such genera as *Capoeta*, *Cyprinus* and *Carassius* appear to be more closely related to the squaliobarbines than do other investigated taxa. Work in preparation (Banister & Howes) seeks to establish monophyletic grouping amongst the barbelled cyprinids. In view of the suspected non-monophyly of so many currently recognized cyprinid assemblages, the reconstruction of ichthyogeographical relationships (eg. Bănărescu, 1973) is fruitless.

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